Seasonal variation in the reproductive biology of the Ring-billed Gull (*Larus delawarensis*)

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ABSTRACT

The reproductive biology of the Ring-billed Gull (Larus delawarensis) was studied on Gull Island, Presqu'ile Provincial Park, Ontario, in 1976 and 1977. Early started clutches (comprising the majority of clutches on Gull Island) in 1977 produced more chicks per nest (2.20 ± 0.09) than late started clutches (0.86 ± 0.13) as a result of reductions in mean clutch size, hatching success and fledging success with date of clutch initiation. Seasonal changes in mean clutch size, hatching success and fledging success also resulted in early clutches, initiated at the peak of clutch starts, producing more chicks per nest (2.34 ± 0.11) than either pre-peak (2.13 ± 0.20) or post-peak (1.82 ± 0.29) clutches. Possible reasons for these trends, including the observed predominance of immature plumaged, breeding gulls in late started areas, are discussed.

Clutches were deserted at night for varying lengths of time from at least 15 April until 10 May, 1977. It is suggested that this nocturnal desertion behaviour resulted in the enhancement of inter- and intra-clutch hatching synchrony in early started areas and further, that this may in part explain the existence of the behaviour in terms of its adaptive significance.

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Dedicated to Mum and Dad

INTRODUCTION

The Ring-billed Gull (Larus delawarensis) is a North American member of the family Laridae, subfamily Larinae. Like many of its close relatives, this gull nests on the ground in insular or isolated mainland colonies and is restricted to a largely inland breeding range consisting of an eastern population centred on the Great Lakes, and a western, prairie population (Southern, 1974).

The population of Ring-billed Gulls in the Great Lakes region has increased dramatically over the past half century (Ludwig, 1974). Ludwig (1968, 1974) attributed this population increase to a variety of factors. In particular he suggested that decreasing Great Lakes water levels in the early 1960's made available large areas of breeding habitat that were previously flooded and furthermore that the establishment and spread of the Alewife (Alosa pseudoharengus) in the Great Lakes increased the availability of food. In addition, the Ring-billed Gull's opportunistic foraging habit (Jarvis and Southern, 1976), longevity, large clutch size and low post-fledge-pre-adult mortality (as a result of short generation time) (Ludwig, 1966, 1974) have been implicated as factors enabling the species' population to 'take advantage' of increases in the availability of nesting habitat and food and thus increase in size.

In addition to estimates of post-fledge-pre-adult mortality and annual adult mortality, the total reproductive success (chicks fledged per pair) of Great Lakes Ring-billed Gulls is a very important parameter in understanding the population dynamics of this species; however, few data are available. Table I.1 summarizes most of the literature (to date) reporting hatching

Table I.1: The Reproductive Success of Ring-billed Gulls in Great Lakes Colonies.

Reference	Lake or Area	Year	Hatching[1] Success	Fledging[2] Success	Total[3] Reproductive Success	Remarks
Emlen, 1956	Mackinack Straits, Michigan	1952, 1953	0.72	0.22	0.67	Estimates based on number of clutches and dead chicks found in areas of colony. Assumed clutch size of 3.0.
Ludwig, 1966	Michigan and Huron	1963, 1964	0.91	0.74	1.74	Estimates based on number of clutches and dead chicks found in areas of colony. Assumed clutch size of 2.96. Used correction factor to account for missing chicks.
Dexheimer and Southern, 1974	Huron	1972	0.45-0.82	0.57-0.91	0.68-1.89	Estimates varied with colony and whether clutch samples were central or peripheral.
Ryder, 1975	Superior	1973	0-0.63	--	--	Estimates varied with clutch size and relative age of adults.
Hunter et al. 1976	Ontario	1972	0.70-0.89	--	--	Estimates varied with colony and date of clutch initiation.
	Erie	1974	0.92	--	--	Lake Erie estimate for 3-egg clutches.
Somppi, 1978	Superior	1977	0-0.83	0.18-0.73	0-1.06	Estimates varied with date of clutch initiation and clutch size.
Haymes and Blokpoel, 1978	Ontario	1977	0.73-0.96	--	--	Estimates varied with age of adults and date of clutch initiation.

[1] Eggs hatched per egg laid
[2] Chicks fledged per egg hatched
[3] Chicks fledged per nest

success (eggs hatched per egg laid), fledging success (chicks fledged per egg hatched) or total reproductive success rates for Great Lakes Ring-billed Gulls. In view of the widespread distribution and numerical abundance of the species, the paucity of data is remarkable. Clearly, a more concerted and systematic effort to determine how well the Ring-billed Gull is reproducing in the Great Lakes, is required in order that we may place in better perspective, the population explosion of this species.

There is considerable variability in the reported reproductive statistics (Table I.1). Dexheimer and Southern (1974) found hatching success to be lower in Ring-billed Gulls nesting on the periphery of the colony compared to central gulls. They also found that wave action reduced the fledging success of peripheral as compared to central chicks. Conversely, Somppi (1978) found no such relationship in her Ring-billed Gull colony. Instead, she found reproductive success to be related to clutch size and time of clutch initiation. More specifically, hatching success was maximized in 3-egg clutches and decreased with the date of clutch initiation. Ryder (1975) aged Ring-billed Gulls by plumage characteristics and found that breeding pairs containing at least one immature gull suffered lower hatching success than mature plumaged pairs. Haymes and Blokpoel (1978) studied known age Ring-billed Gulls and found that hatching success decreased with date of clutch initiation in pairs containing at least one gull less than four years old, but remained the same in older pairs. Vermeer (1970) studied Ring-billed Gulls in Alberta (at Miquelon Lake) and found that fledging success, but not hatching success, decreased with the date of clutch initiation.

In addition to relationships concerning reproductive statistics, other trends of interest have been noted. Young Ring-billed Gulls were found to initiate clutches later in the season, and closer to the periphery of the

colony (Ryder, 1975; Haymes and Blokpoel, 1978) and to produce generally smaller clutches irrespective of clutch start time (Haymes and Blokpoel, 1978) compared to older gulls. Ryder (1975) found no relationship between the relative age of the Ring-billed Gull pair and clutch size up to 3 eggs. However, he noted that mature pairs produced more, large clutches ($\geq$4-egg) than pairs containing at least one immature plumaged gull. He also found that mean clutch size decreased with date of clutch initiation irrespective of the relative age of the pair.

Similar relationships have been found in other gull species. In general, reproductive success decreases with the date of clutch initiation or is maximal when the date of clutch initiation coincides with the peak of clutch starts for the colony as a whole (e.g., for Herring Gulls (L. argentatus): Brown, 1967; Kadlec and Drury, 1968; Parsons, 1975a; Lesser Black-backed Gulls (L. fuscus): Brown, 1967; Glaucous-winged (L. glaucescens) and California Gulls (L. californicus): Vermeer, 1963, 1970; Black-headed Gulls (L. ridibundus): Patterson, 1965). The timing of breeding and reproductive success have been found to be related to the age or breeding experience of the parent gulls. Young or inexperienced gulls tend to nest later in the breeding season, produce smaller clutches, and suffer reduced hatching and fledging success as compared to older or more experienced gulls (e.g., for Kittiwakes (Rissa tridactyla): Coulson and White, 1958, 1961; Herring Gulls: Chabrzyk and Coulson, 1976).

A variety of factors have been implicated as causes of the relationships outlined above. Reduced breeding synchrony may cause gulls nesting before or after the peak of clutch starts to suffer increased egg and chick predation (Patterson, 1965; Parsons, 1975a). Further, very early or late breeders may be reproducing at a time when the availability of food or the general quality

of the environment (in terms of climate, vegetation, the availability of nest sites and many other factors) are not optimal (cf. Perrins, 1970). On the other hand, gulls reproducing late in the season may be in general young or inexperienced individuals, renesters, or individuals that have changed their mates in the preceding year, and, as a result of either factor, suffer reduced reproductive success (cf. Coulson and White, 1958; Coulson, 1966; Parsons, 1975a).

With the aforementioned literature in mind, I decided to study the reproductive biology of the Ring-billed Gull in order to attempt to answer the following questions:

1. What is the reproductive success of the Ring-billed Gull in a Great Lakes colony?
2. Does this reproductive success vary with the date of clutch initiation within the colony?
3. If so, what possible factors are responsible for the observed relationship?

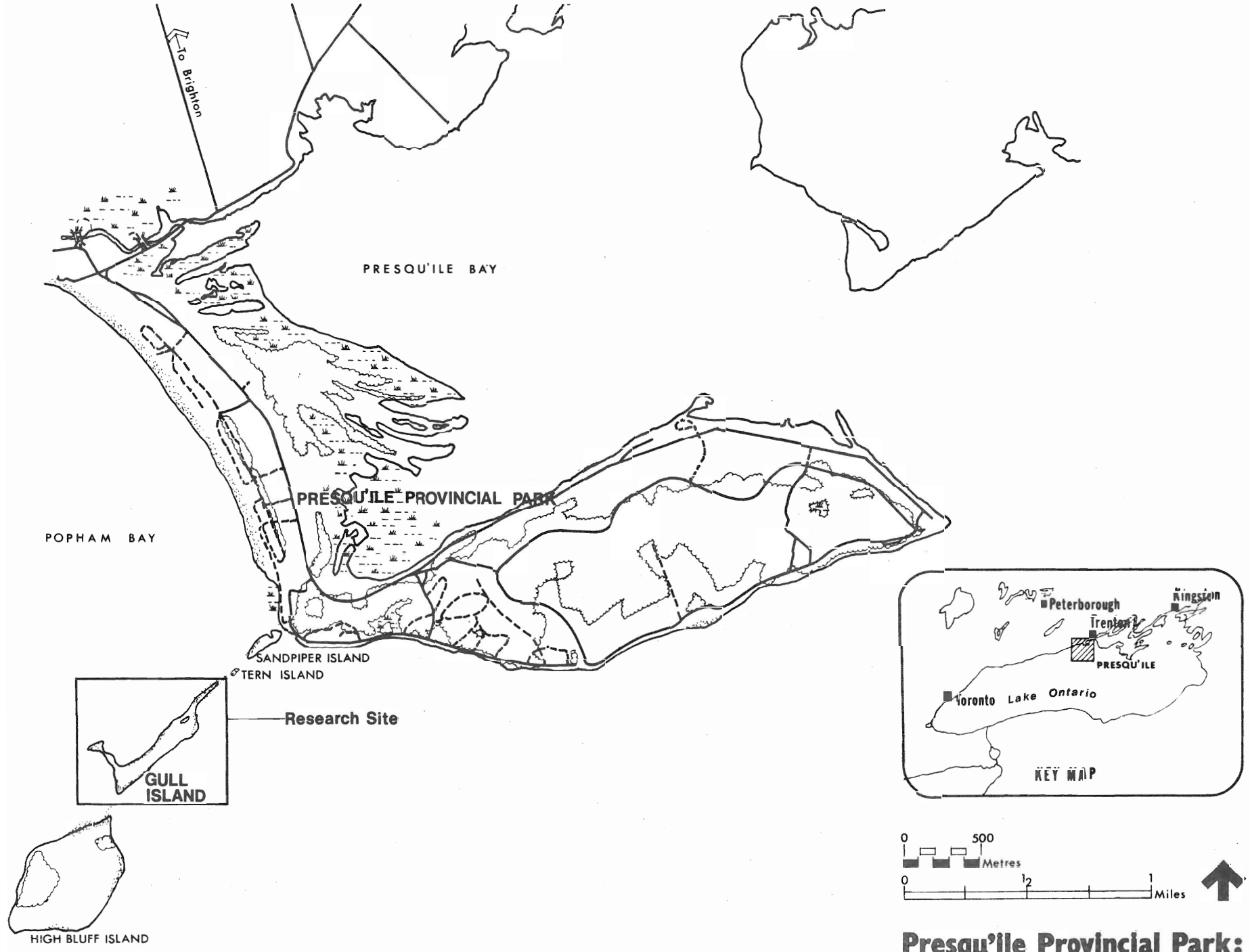
METHODS

For a variety of logistic reasons including easy accessibility and personal familiarity with the general site, I decided to study the colony of Ring-billed Gulls located on Gull Island, Presqu'ile Provincial Park, Brighton, Ontario (Figure 1A). The study took place during the 1976 and 1977 breeding seasons.

1. Site description

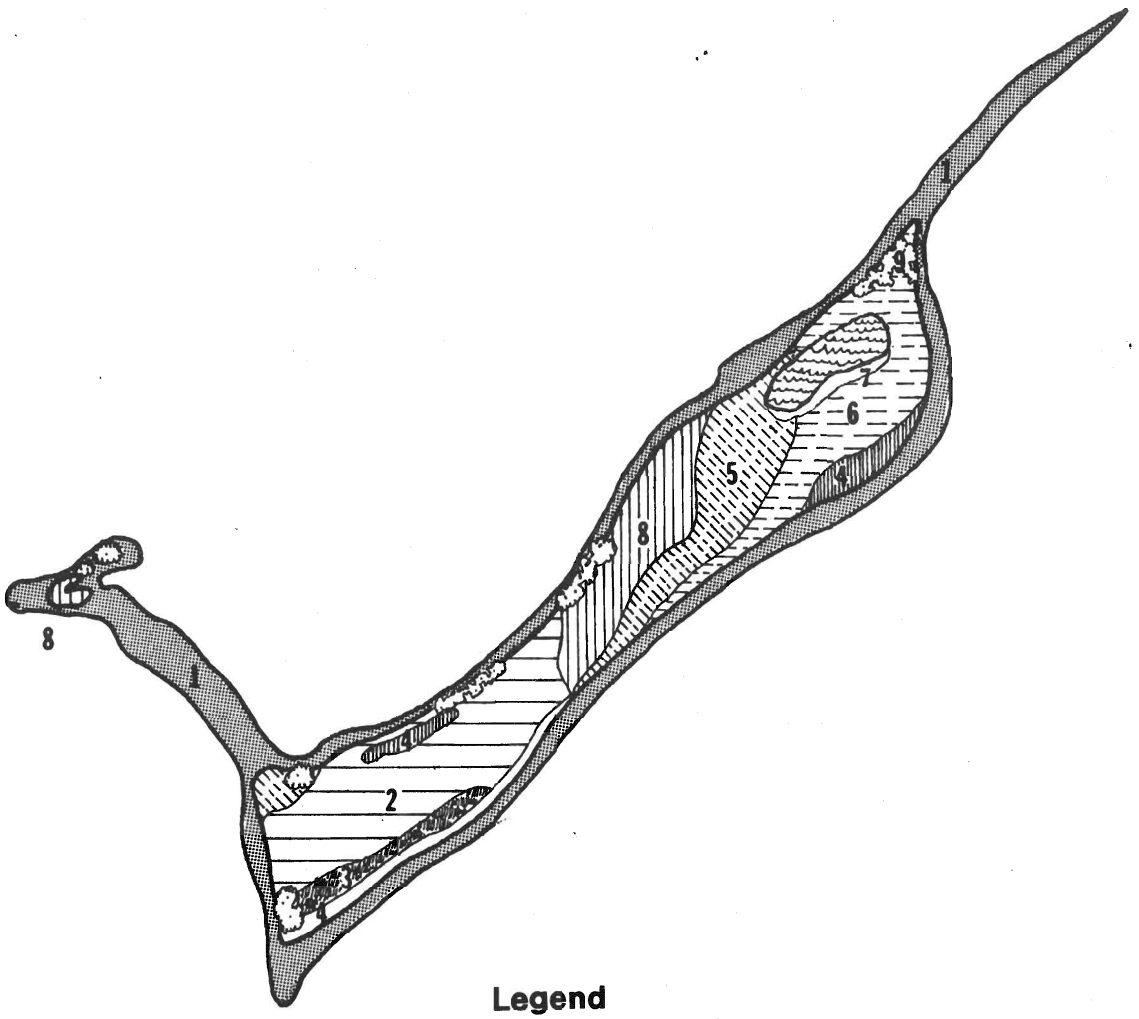
Gull Island (44° 59'00" N, 77° 44'21" W) referred to by Ludwig (1974) as "The Bluffs", lies approximately 250 metres offshore in Lake Ontario. A limestone pebble beach surrounded the island and enclosed a depressed, generally flat, vegetated area. Dominant annual and perennial plant species were: grasses (Graminae), nettles (Urtica spp.), Pigweed (Chenopodium sp.), Sow-Thistle (Sonchus sp.), mustards (Brassica spp.) and Smartweed (Polygonum sp.) (Figure 1B). Several tree and shrub species including Willow (Salix sp.), Elm (Ulmus sp.), Elderberry (Sambucus sp.) and Dogwood (Cornus sp.) occurred along the north shore and at the southwest tip of the island. A pond was located in the eastern part of Gull Island and was probably a permanent feature (H. Richards, pers. comm.). Due to high Lake Ontario water levels in 1976, the pond expanded westward and flooded an area of approximately 9000 square metres that had previously been used as Ring-billed Gull nesting habitat (J. Chardine, pers. obs.). However, in 1977, the pond was reduced to its former dimensions of approximately 60 metres long by 25 metres wide (area: 1400 square metres) and exposed a mud-flat area.

Figure 1A: Map of research site.



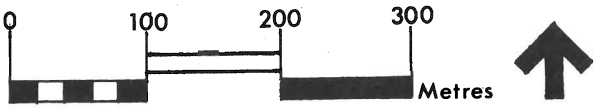
Presqu'ile Provincial Park: Research Site

Figure 1B: Map of vegetation on Gull Island



Legend

1. Limestone Pebble Beach
2. Grasses, Pigweed, Sow–Thistle, Smartweed
3. Grasses
4. Mustard
5. Smartweed, Nettle
6. Nettle Grasses, Smartweed, Jewelweed
7. Arrowhead, Bur– reed
8. Nettle, Grasses
9. Elm, Willow, Elderberry



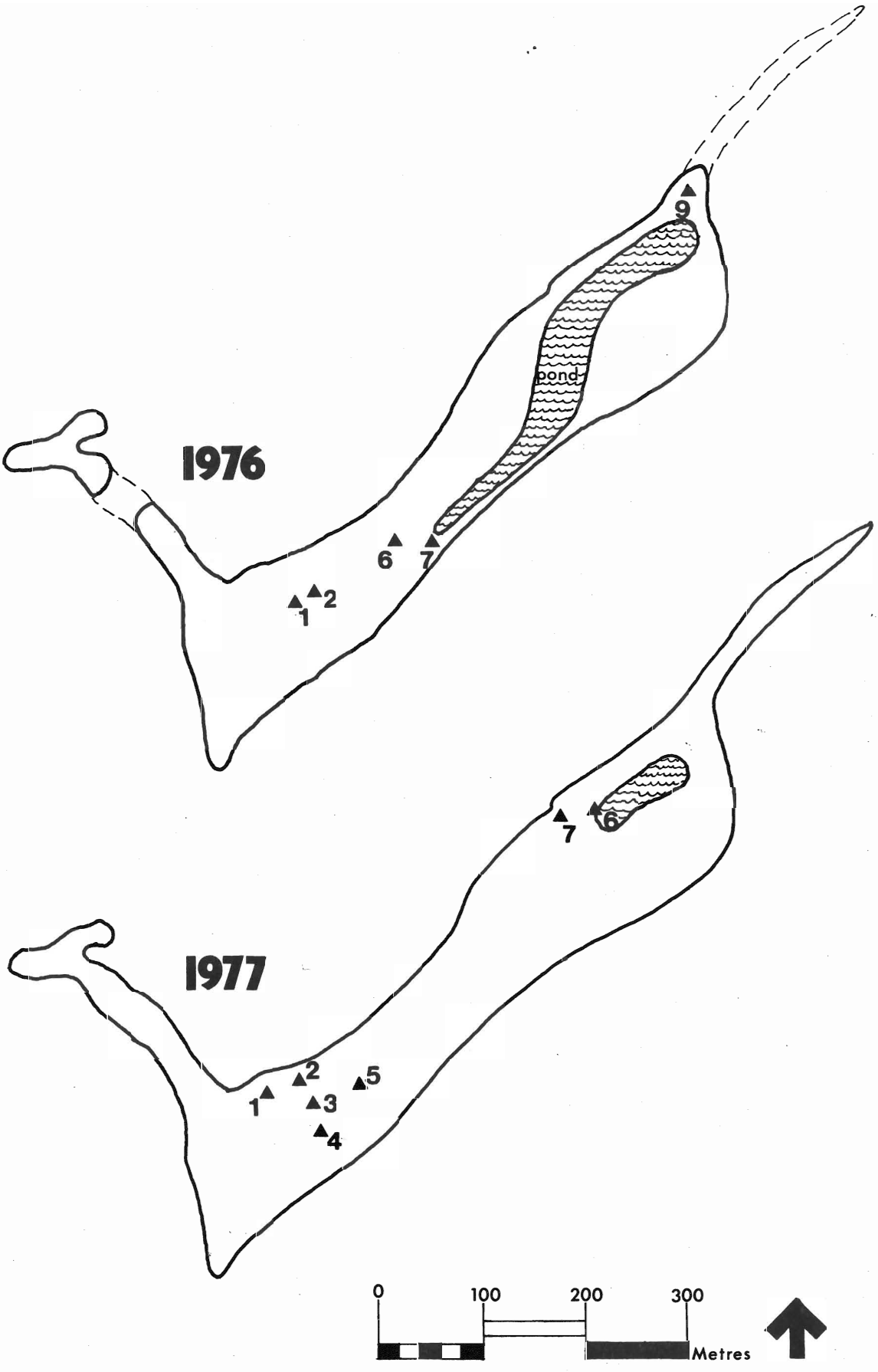
Gull Island: Vegetation

In the two years of my study, Ring-billed Gulls nested on approximately 4.5 ha of the 5.3 ha total island area. Most Ring-billed Gulls nested within the vegetated interior of the island, however, considerable numbers also used the pebble beach. Various estimates of the numbers of breeding pairs of Ring-billed Gulls nesting on Gull Island have been made. Ludwig (1974) estimated that 23,000 pairs nested on Gull Island in 1967, while Blokpoel (1977), using aerial photography, estimated that 23,707 ± 2,326 (1 standard error of N) pairs were nesting on 13 May, 1976. Approximately 27,500 Ring-billed Gull nests were counted on 26 May, 1978 (H. Blokpoel, pers. comm.).

Approximately 60 pairs of Herring Gulls nested mainly on the periphery of the Ring-billed Gull colony and on the north-west spit. Three pairs of Common Terns (Sterna hirundo) nested in a small area south of the pond, in 1977. The Common Tern population on Gull Island has declined, at least over the past 5 years (J. Chardine, pers. obs.; H. Richards, pers. comm.) despite recent attempts to increase numbers by management (R. Morris, pers. comm.). Black-crowned Night Herons (Nycticorax nycticorax) nested in some of the trees and shrubs on the island during 1976 and 1977. Although accurate nest counts were not made, the species numbered approximately 30-40 breeding pairs during this study.

The position of each study area within the Gull Island Ring-billed Gull colony, from 1976 and 1977, are shown in Figure 1C. The first and major wave of clutch starts in both years were represented in early started areas. These study areas were chosen only in vegetated areas of the colony where vegetation structure was approximately similar. After the peak of clutch starts occurred in early started areas, the island was systematically surveyed for synchronous aggregations of clutches forming the late started

Figure 1C: Position of study areas from 1976 and 1977 on Gull Island



Study Area Locations On Gull Island

sample. The vegetation structure within late started areas was approximately similar to that in early started areas. The substrate in all study areas was soil usually bound with low-lying vegetation such as grasses. No heterospecific breeding birds were located either in or on the boundary of any study area.

2. Collection of reproductive success and chick growth data

Visits to Gull Island were made by boat or canoe as frequently as possible, at approximately the same time each day, weather and lake conditions permitting. In 1976, the visitation rate averaged 1 visit every 2 days between 20 April and 2 August while in 1977, good weather throughout the season allowed the island to be visited almost everyday from 11 April to 17 July.

Standard procedures upon each visit to the study areas were as follows: All new nests were marked with a numbered wooden stake placed approximately 15 cm from the outside of the nest cup. All new eggs in each nest were marked according to laying order where known with a non-toxic, magic marker. All eggs were checked to determine condition, and pip date. New Chicks were banded with standard aluminium USFWS bands (Size 5), usually within 1 day of hatching. Live and dead chick inventories of each study area were taken whenever chicks were weighed. Chicks were considered fledged if they reached the age of 30 days post hatch. Prior to the expected date of hatching, a chicken wire fence (2.5 cm mesh size, 60 cm high) supported by wooden stakes, was erected around each study area in order to prevent chicks from wandering large distances from their nest site upon my visits.

All chicks from clutches initiated before 22 April, 1977 and a random sample from clutches initiated between 22 and 30 April, 1977, in early

started areas were weighed everyday until 7 days old and then less frequently (every 2-5 days) until the taking of the final weight at 30 days or older. In addition, all chicks from clutches initiated after 12 May, 1977, in late started areas, were similarly weighed. Chicks were placed in a plastic bag and weighed using various sizes of Pesola spring balances (supplied by Bleitz Wildlife Foundation, Hollywood, California).

Reproductive success data were transferred to computer cards and analysed using a programme written by Janet Glazebrook (Computer Science, Brock University) and Peter Courtney.

3. Collection of incubation attentiveness data

Incubation attentiveness, in this thesis, is defined as the amount of time per hourly period, spent by a pair of gulls in the act of incubating their eggs. The incubation attentiveness of random samples of Ring-billed Gulls from study areas 1, 2, 3, 4, 6 and 7 in 1977, was monitored continuously from the egg laying period to the hatching of the first chick in a clutch. Two, twenty-pen Esterline Angus event recorders (Model A620X), each powered by a 12-volt car battery, and connected to micro-switch devices placed over the nest, were used following the methods of Morris and Hunter (1976). The monitoring of study areas 1, 2, 3 and 4 began on 15 April 1977, and proceeded until 26 May, 1977. Study areas 6 and 7 were monitored from 17 May, 1977 until 18, June, 1977.

4. Statistical analysis

Seigel (1956) and Snedecor and Cochran (1967) were used as statistical references throughout. Hypotheses involving reproductive and other proportion statistics were tested using a 2 x 2 contingency table and calculating either

a Chi-squared statistic, with Yates correction for continuity (χ^2_c) or the Fisher Exact Probability. The choice of either test depended on sample size and cell frequencies in the contingency table (cf. Seigel, 1956, p. 110). The above tests are used frequently throughout this thesis. All other statistical tests are specified at the time of use. Full statistical significance is achieved when the probability (p) of obtaining a particular result in a given test, under the null hypothesis, is ≤ 0.05. When $0.05 < p \leq 0.10$ in a given test, marginal significance is considered to be achieved.

RESULTS

SECTION 1 The reproductive success of the Ring-billed Gull nesting on Gull Island in 1976 and 1977

I Clutch start distributions

Due to the similarity of study areas 1, 2, 6 and 7 in 1976 and 1, 2, 3, 4 and 5 in 1977, with respect to vegetation structure, clutch start distributions and nesting density (Tables 1A and 1B), data from these areas, within each year, were pooled. This formed two comparable groups of nests that will henceforth be referred to as early clutches within early started study areas. Using the above criteria, data from study areas 6 and 7 in 1977, were also pooled to form a group of late clutches within late started study areas. Study area 9 from 1976 represents the sole sample of late started nests from that year.

Nest start distributions for early and late started study areas from 1977 are shown in Figures 2A and 2B. Equivalent distributions for early and late started study areas from 1976 are not shown due to their imprecise nature; however, the salient and most reliable points (production dates) of the 1976 distributions together with those for 1977 can be seen in Tables 1A and 1B.

First egg dates in early started study areas were 12 April in 1976 and 9 April in 1977. Fifty percent of all early started clutches were initiated on or before 28 April in 1976 and 26 April in 1977. Late started study areas in 1976 and 1977 were also similar in their chronology. First egg dates in late started study areas were 12 May in 1976 and 2 May in 1977. Fifty percent

TABLE 1A: 1976 Study Area Data

	Area Number	Area (m^2)	Clutches (n)	Nest Density (nests/m^2)	Production Dates	
					First Egg	50% Egg Production
Early Started Areas	1	77	42	0.55	12 April	29 April
	2	77	48	0.62	12 April	29 April
	6	38	20	0.53	18 April	29 April
	7	60	44	0.73	20 April	29 April
	Total	252	154	0.61	12 April	29 April
Late Started Areas	9	61	39	0.64	12 May	21 May

TABLE 1B: 1977 Study Area Data

	Area Number	Area (m^2)	Clutches (n)	Nest Density (nests/m^2)	Production Dates	
					First Egg	50% Egg Production
Early Started Areas	1	49	23	0.47	10 April	27 April
	2	42	20	0.48	9 April	30 April
	3	70	33	0.47	16 April	27 April
	4	30	14	0.47	19 April	30 April
	5	37	23	0.67	20 April	28 April
	Total	228	113	0.50	9 April	28 April
Late Started Areas	6	59	18	0.31	12 May	21 May
	7	59	24	0.41	2 May	18 May
	Total	118	42	0.36	2 May	19 May

Figure 2A: The clutch start distribution of early started areas from 1977.

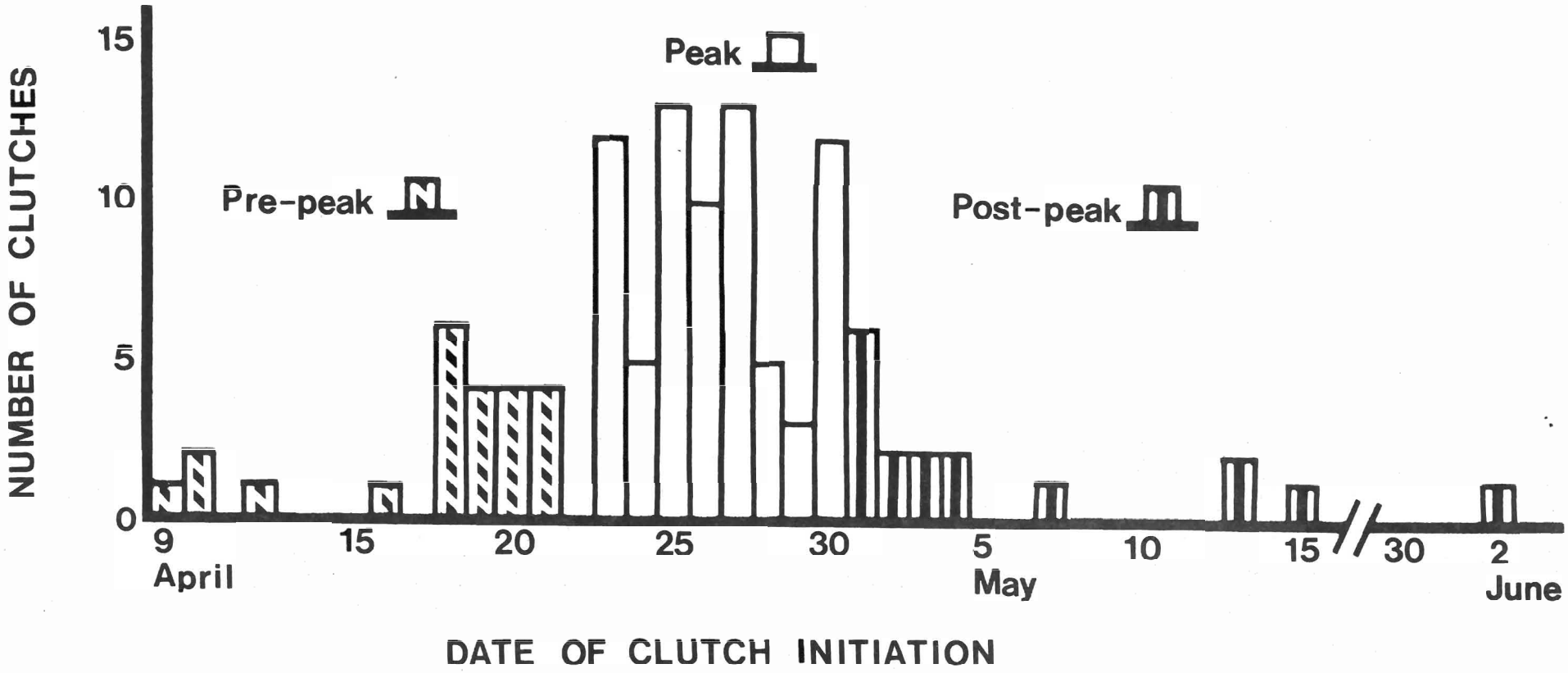
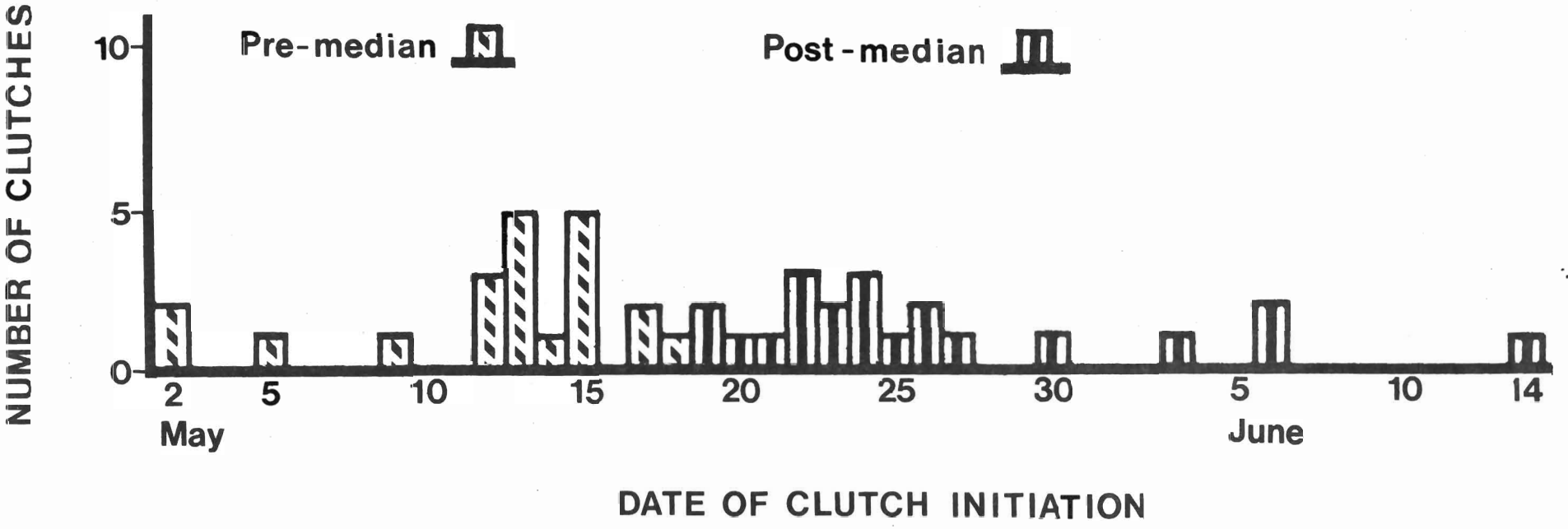

NUMBER OF CLUTCHES
15
10
5
0
Peak
Pre-peak
Post-peak
9
April
15
20
25
30
5
May
10
15
30
2
June
DATE OF CLUTCH INITIATION

Figure 2B: The clutch start distribution of late started areas from 1977.


NUMBER OF CLUTCHES
10
5
0
Pre-median
Post-median
2
May
5
10
15
20
25
30
5
June
10
14
DATE OF CLUTCH INITIATION

of all late started clutches were initiated on or before 21 May in 1976 and 18 May in 1977. Exceptionally warm and dry weather in April 1977 may have caused the earlier dates for this year. Both Common Terns and Ring-billed Gulls at a Port Colborne colony were approximately 1 week ahead of their 1976 chronology, in 1977. (P. Courtney pers. comm.)

In order to study seasonal trends in reproductive success, the clutch start distributions for early and late started study areas from 1977 were divided into groups of nests according to the date of clutch initiation. Pre-peak (9-22 April), peak (23-30 April) and post-peak (1 May-1 June) groups of nests were identified from the early nest start distribution (cf. Figure 2A). No obvious peak was present in the nest start distribution for late started study areas (cf. Figure 2B), therefore, nests were arbitrarily split into two groups at the date when 50% of the clutches were initiated (18 May). Clutches initiated between 2-18 May will be termed pre-median, while clutches initiated after 18 May will be termed post-median. In order to avoid the possibility of bias resulting from

1. a disproportionate number of clutches from any one study area being represented within any one time period, and
2. between study area differences in reproductive success (hatching and fledging success),

study areas were treated separately as well as together when investigating seasonal trends in reproductive success.

II: Plumage of birds nesting in 1976 and 1977 study areas

All Ring-billed Gulls nesting in the 1976 study areas and the early started study areas from 1977 were in adult plumage (cf. Godfrey, 1966; pages 180-181). However, in 1977, immature plumaged gulls nested in late started study areas 6 and 7 (Table 2). A Ring-billed Gull was classed as immature (after Bent, 1921) if it displayed one or more of the following plumage characteristics:

1. buffy wing coverts,
2. full, black subterminal tail band,
3. remnants of the subterminal band in the form of one or more subterminal black dots on the rectrices.

A bird displaying a combination of the above characteristics together with buffy neck feathers, little leg or bill colour and a generally drab appearance was considered to be a 1 year old bird (Bent, 1921), none of which were seen to breed in 1977.

All immature plumaged birds seen breeding in 1977 were considered to be 2 or 3 years old (Bent, 1921). It is recognized, however, that considerable variability in immature Ring-billed Gull plumage characteristics exists and thus the immature birds referred to in this study represent a distribution of ages with a mean lower than that for adult plumaged individuals. Of the 42 pairs nesting in both late started study areas, a total of 31 (74%) contained at least one immature plumaged individual (cf. Table 2).

Table 2: Pair types nesting in late started study areas from 1977

Area number	Clutches (n)	Pair Type[1] (n), proportion of total pairs					
		A x A	A x ?[2]	A x B	B x ?	B x B	? x ?
6	18	(1)0.05	(0)0.0	(8)0.44	(7)0.39	(2)0.11	(0)0.0
7	24	(2)0.08	(4)0.17	(3)0.13	(10)0.42	(1)0.04	(4)0.17
Total	42	(3)0.07	(4)0.10	(11)0.26	(17)0.41	(3)0.07	(4)0.10

[1]A x A--Adult-Adult pair

A x B--Adult-Immature pair

B x B--Immature-Immature pair

[2]Age unknown

III: Clutch size distributions

Clutch Size distributions for early and late started study areas from 1976 and 1977 are in Table 3A. A modal clutch size of three eggs was found in early and late started clutches from both years. Two-egg clutches comprised 6.5% (n = 10) of all early started clutches in 1976 and 4.4% (n = 5) of same in 1977. Late started clutches in both 1976 and 1977 contained a significantly higher proportion of two eggs than their early started counterparts (1976: $\chi^2_c = 10.31$, $p < 0.01$; 1977: $\chi^2_c = 11.04$, $p < 0.01$). In 1976, 25.6% (n = 10) of all late started clutches contained 2 eggs while in 1977, 23.8% (n = 10) of late started clutches were 2-egg clutches.

Four-egg clutches comprised 1.3% (n = 2) and 8.0% (n = 9) of all early started clutches in 1976 and 1977 respectively. Only one, 4-egg clutch was laid in late started study areas (in 1977). One-egg clutches were laid predominantly in the late started study areas, and comprised 12.8% (n = 5) and 11.9% (n = 5) of all late started clutches in 1976 and 1977 respectively. Five and 6-egg clutches were excluded from subsequent clutch size analysis because of their rarity (1.2% (n = 4) of clutches studied) and the possibility that they were produced by more than one female gull (cf. Ryder, 1975).

The seasonal trend in clutch size distributions within the early and late started study areas from 1977 are in Table 3B. Within the early started study areas, a decline in the mean clutch size with season is evident. Four 4-egg clutches laid on or before 22 April produced a mean clutch size greater than three eggs for the pre-peak time period. Two 2-egg clutches and one 1-egg clutch offset the four 4-egg clutches laid in the peak period to produce a mean clutch size of 3.00. Three 2-egg clutches reduced the mean clutch size below three eggs in the post-peak time period. Similarly, mean clutch size

TABLE 3A: Clutch size distribution for early and late started areas from 1976 and 1977

		Clutch Size (n)						Mean Clutch Size ± S.E.
		1	2	3	4	5	6	
Early Started Areas	1976	0	10	140	2	2	0	2.97 ± 0.03
	1977	1	5	97	9	0	1	3.04 ± 0.05
Late Started Areas	1976	5	10	24	0	0	0	2.49 ± 0.12
	1977	5	10	25	1	1	0	2.60 ± 0.13

TABLE 3B: Seasonal trend in clutch size distribution and mean clutch size within early and late started areas from 1977

	Date Clutches Initiated	Clutch Size[1] (n)				Mean Clutch Size ± S.E.
		1	2	3	4	
Early Started Areas	9-22 April Pre-peak	0	0	18	4	3.18 ± 0.08
	23-30 April Peak	1	2	66	4	3.00 ± 0.04
	1 May-1 June Post-peak	0	3	13	1	2.81 ± 0.10
Late Started Areas	2-18 May Pre-median	0	3	17	1	2.91 ± 0.10
	19 May-14 June Post-median	5	7	8	0	2.15 ± 0.18

[1]Analysis excludes 5 and 6-egg clutches.

decreased with season in late started study areas. Three 2-egg clutches laid in the pre-median time period reduced the mean clutch size below three eggs. A relatively high proportion of 2-egg and 1-egg clutches laid in the post-median time period reduced the mean clutch size to well below three eggs.

IV: The relationship between date of clutch initiation and reproductive success

(a) Hatching success

Hatching success, in this thesis, is defined as the proportion of eggs laid that subsequently hatch (i.e., Hatching success = Number eggs hatched/ number eggs laid). Hatch/Lay is used in the tables as a short form for hatching success.

Table 4 displays hatching success data for 1976 and 1977 respectively. In both years of study, early started clutches hatched with a significantly higher success than their late started counterparts, (1976: $\chi_c^2 = 11.70$, $p < 0.005$; 1977: $\chi_c^2 = 21.36$, $p < 0.005$).

Tables 5A and 5B display the seasonal trend in hatching success within the early and late started study areas from 1977. A separate analysis of 3-egg clutches was done in order to investigate seasonal trends in hatching success while keeping clutch size constant. Generally, peak clutches hatched with greater success than pre-peak clutches, when early started areas were considered separately and when either all clutch sizes or just 3-egg clutches were considered (Table 5A). This trend obtained in areas 1, 2 and 5 but on only two occasions were differences significant (Area 1, all clutch sizes: $\chi_c^2 = 9.65$, $p < 0.005$; 3-egg clutches: $\chi_c^2 = 6.28$, $p < 0.025$). When data from each early started study area and clutch size were pooled, the hatching success

TABLE 4: Hatching success in early and late started areas from 1976 and 1977

		Area number	Eggs Laid (n)	Eggs Hatched (n)	Hatch/Lay
Early Started Areas	1976	1	124	115	0.93
		2	143	121	0.85
		6	59	57	0.97
		7	132	111	0.84
		Total	458	404	0.88
	1977	1	73	55	0.75
		2	60	48	0.80
		3	98	81	0.83
		4	44	41	0.93
		5	69	61	0.88
		Total	344	206	0.83
Late Started Areas	1976	9	97	72	0.74
	1977	6	45	30	0.67
		7	64	37	0.58
		Total	109	67	0.61

Table 5A: Seasonal trend in hatching success within early started areas from 1977.

Date Clutches Initiated	Area # 1	2	Clutches (n), Hatch/Lay 3	4	5	All
All Clutch Sizes						
9-22 April pre-peak	(7)0.52	(4)0.75	(7)0.87	(2)1.00	(3)0.78	(23)0.74
23-20 April peak	(13)0.90	(14)0.81	(21)0.80	(8)0.96	(17)0.94	(73)0.87
1 May-1 June post-peak	(3)0.78	(2)0.83	(5)0.86	(4)0.82	(3)0.67	(17)0.80
3-Egg Clutches						
9-22 April pre-peak	(5)0.60	(4)0.75	(5)0.93	(1)1.00	(3)0.78	(18)0.78
23-30 April peak	(11)0.94	(12)0.89	(20)0.82	(6)1.00	(17)0.94	(66)0.90
1 May-1 June post-peak	(3)0.78	(2)0.83	(4)1.00	(1)0.67	(3)0.67	(13)0.82

Table 5B: Seasonal trend in hatching success within late started areas from 1977

Date Clutches Initiated	Area # 6	Clutches (n), Hatch/Lay 7	All
All Clutch Sizes			
2-18 May pre-median	(7)0.55	(14)0.59	(21)0.57
19 May-14 June post-median	(11)0.76	(10)0.57	(21)0.67
3-Egg Clutches			
2-18 May pre-median	(4)0.50	(13)0.56	(17)0.55
19 May-14 June post-median	(4)1.00	(4)0.67	(8)0.83

of peak clutches was significantly higher ($\chi_c^2 = 6.62$, $p < 0.025$) than pre-peak clutches. When only 3-egg clutches were considered, peak clutches again hatched with a significantly higher success than pre-peak clutches ($\chi_c^2 = 4.58$, $p < 0.05$).

Peak clutches also in general hatched more successfully than post-peak clutches, but in only one instance was the difference even marginally significant (Area 5, all clutch sizes and 3-egg clutches, $\chi_c^2 = 3.72$, $0.05 < p < 0.10$) Table 5A). When data from all early started study areas were pooled either for all clutch sizes or 3-egg clutches, peak clutches hatched with a higher success than post-peak clutches but the differences were not significant (χ_c^2 tests, $p > 0.10$).

In late started study areas from 1977 (Table 5B), clutches generally hatched with a higher success later in the season (post-median). In one out of four instances the difference was significant. (Area 6, 3-egg clutches, $p = 0.007$, Fisher Exact Probability Test).

Considering the late started study areas pooled, 3-egg clutches hatched significantly better in the post median period ($\chi_c^2 = 4.56$, $p < 0.05$). When all clutch sizes were pooled, χ_c^2 tests revealed no significant differences in the hatching success of pre- and post median clutches ($p > 0.10$).

(b) Causes of egg failure

Table 6 displays the seasonal trend in causes of egg failure from the 1976 and 1977 study areas.

The most common cause of egg failure in both early and late started clutches, from both years of study, was loss due to addling. An egg was considered addled if it remained in the nest, intact, and did not subsequently hatch, or exhibited a liquid, "sloshy" feel when very gently moved from side to side.

TABLE 6: Causes of egg failure in early and late started study areas from 1976 and 1977

Causes of Egg Failure	Early Started Areas 1976 (n), % of Eggs Lost	Early Started Areas 1977 (n), % of Eggs Lost	Late Started Areas 1976 (n), % of Eggs Lost	Late Started Areas 1977 (n), % of Eggs Lost
Addled[1]	(39), 72	(31), 54	(13), 52	(17), 40
Disappeared	(7), 13	(2), 5	(5), 20	(3), 7
Cracked	(0),	(1), 2	(1), 4	(1) 2
Died While Pipping	(4), 7	(9), 16	(2), 8	(4), 10
Rolled From Nest	(0),	(7), 12	(0),	(8), 19
Deserted	(0),	(0),	(2), 8	(3), 7
Pecked	(2), 4	(0),	(0),	(0),
Unknown	(0),	(0),	(0),	(0),
Worker Error	(2), 4	(1), 2	(2), 8	(2), 5
Predated	(0),	(6), 10	(0),	(4), 10
Buried in Nest	(0),	(1), 2	(0),	(0),

[1]Egg remained intact, in nest, until other eggs hatched or exhibited liquid centre.

In 1976, 31 addled eggs were broken open and the egg contents evaluated on the basis of embryo development and degree of bacterial degradation. Of the 31 addled eggs examined, 24 (77%) contained no visible embryo, 2 (7%) contained embryos in their last week of development and 5 (16%) were indistinguishable due to bacterial deterioration.

All other causes of egg failure were at low levels and seasonal trends were not obvious. Generally, the incidence of cracking, rolling from nest, disappearance and desertion were proportionately higher in late started study areas. Predation, pecking and death while pipping occurred proportionately more often in early started study areas.

The decreased hatching success observed in late started study areas from both years of study (cf. Table 4) was associated with a disproportionate increase in egg failures other than addling (Data from both years pooled: $\chi^2_c = 4.65$, $p < 0.05$ when worker error category included in comparison; $\chi^2_c = 3.87$, $p < 0.05$ when worker error excluded from comparison).

(c) Fledging success

Fledging success, in this thesis, is defined as the proportion of chicks hatching that subsequently reach the age of 30 days (i.e., Fledging success = Number of chicks surviving to 30 days/number of eggs hatched). It is recognized that the age at first flight for Ring-billed Gulls occurs approximately one week after the age at which chicks are considered fledged here. However, since Gull Island Ring-billed Gull chicks have been observed in free flight at 31 days of age and at this age chicks are capable of escaping from the fenced study areas, chick survival to 30 days was considered a good estimate of chick fledging potential. Fledge/hatch is used in the tables as a short form for fledging success.

TABLE 7: Fledging success in early and late started areas from 1977

	Area	Eggs Hatched (n)	Chicks Fledged[1] (n)	Fledge/Hatch
Early Started Areas	1	55	49	0.89
	2	48	42	0.88
	3	81	69	0.85
	4	41	35	0.85
	5	61	54	0.89
	Total	286	249	0.87
Late Started Areas	6	30	13	0.43
	7	37	23	0.62
	Total	67	36	0.54

[1]Chicks were considered fledged if they survived to 30 days of age.

Due to a lower visitation rate in 1976 than in 1977, and the generally larger 1976 study areas, an analysis of chick 'disappearance' with age showed that chicks were not reliably caught for inventory after 23 days of age. Thus, fledging data from 1976 early and late started study areas were not included in this thesis as comparisons can in no way be made with other fledging success data reported here.

Table 7 displays fledging success data for early and late started study areas from 1977. Early started chicks fledged significantly better than late started chicks ($\chi^2_c = 36.66$, $p < 0.001$). Tables 8A and 8B display the seasonal trend in fledging success within the early and late started study areas from 1977. A separate analysis of 3-egg clutches was done in order to investigate seasonal trends in fledging success while keeping the size of the clutch from which the chicks originated, constant.

Generally, peak chicks fledged with greater success than pre-peak chicks, when early started study areas were considered separately and when either all clutch sizes were pooled or just 3-egg clutches were considered (Table 8A). This trend obtained in study areas 1, 2 and 5 but in no instances were the differences statistically significant (χ^2_c tests, $p > 0.10$). When data from each early started study area and clutch size were pooled, the fledging success of pre-peak and peak chicks was identical. When only 3-egg clutches were considered, peak chicks fledged more successfully than pre-peak chicks although a χ^2_c test revealed no significant difference ($p > 0.10$).

Peak chicks also, in general, fledged more successfully than post-peak chicks but again the differences were not great. Only a single statistically significant difference was found (Area 1, all clutch sizes and 3-egg clutches: $\chi^2_c = 4.54$, $p < 0.05$). When data from all early started study areas were

Table 8A: Seasonal trend in fledging success within early started areas from 1977

Date Clutches Initiated	Clutches (n), Fledge/Hatch Area # 1	2	3	4	5	All
All Clutch Sizes						
2-33 April pre-peak	(7)0.92	(4)0.78	(7)0.90	(2)0.86	(3)0.86	(23)0.88
23-30 April peak	(13)0.94	(14)0.91	(21)0.84	(8)0.80	(17)0.92	(73)0.88
1May-1 June post-peak	(3)0.57	(2)0.80	(5)0.83	(4)0.82	(3)0.67	(17)0.79
3-Egg Clutches						
9-22 April pre-peak	(5)0.89	(4)0.78	(5)0.86	(1)0.67	(3)0.86	(18)0.83
23-30 April peak	(11)0.94	(12)0.91	(20)0.84	(6)0.78	(17)0.92	(66)0.88
1 May-1 June post peak	(3)0.57	(2)0.80	(4)0.83	(1)0.67	(3)0.67	(13)0.75

Table 8B: Seasonal trend in fledging success within late started areas from 1977

Date Clutches Initiated	Clutches (n), Fledge/Hatch Area # 6	7	All
All Clutch Sizes			
2-18 May pre-median	(7)0.64	(14)0.75	(21)0.71
19 May-14 June post-median	(11)0.32	(10)0.38	(21)0.34
3-Egg Clutches			
2-18 May pre-median	(4)0.33	(13)0.73	(17)0.64
19 May-14 June post-median	(4)0.50	(4)0.50	(8)0.50

pooled either for all clutch sizes or 3-egg clutches, peak chicks fledged more successfully than post-peak chicks, although in only the latter instance was the difference even marginally significant (3-egg clutches: $\chi^2_c = 2.94$, $0.05 < p < 0.10$).

In late started study areas from 1977 (Table 8B), chicks generally fledged with greater success in the pre-median time period. When all clutch sizes were pooled, pre-median chicks from both study areas 6 and 7 fledged with a greater success than their post-median counterparts, although χ^2_c tests revealed no significant differences ($p > 0.10$). When all clutch sizes and both late started study areas were pooled, pre-median chicks fledged with a significantly higher success than post-median chicks ($\chi^2_c = 7.80$, $p < 0.01$).

When only 3-egg clutches were considered, Areas 6 and 7 differed in the proportion of chicks fledging from pre- and post-median nests. In area 6, post-median chicks fledged more successfully than pre-median chicks although the difference was not statistically significant ($p > 0.10$, Fisher Exact Probability Test). The reverse situation obtained in area 7 whereby pre-median chicks followed the trend found when all clutch sizes were pooled, and fledged more successfully than post-median chicks; however, again the difference was not statistically significant ($p > 0.10$, Fisher Exact Probability Test).

When data from both late started study areas were pooled, and just 3-egg clutches considered, pre-median chicks fledged with a higher success than post-median chicks although a χ^2_c test revealed no significant difference ($p > 0.10$).

(d) Total reproductive success

Total reproductive success, in this thesis, is represented in two ways. Where appropriate, the mean number of chicks fledged per nest (mean fledge/nest = number of chicks fledged/number clutches) is used, while elsewhere, the number of chicks fledged per egg laid (fledge/lay = number of chicks fledged/number of eggs laid) represents total reproductive success.

In only a few instances was statistical analysis applied to total reproductive success data because rigorous statistical analysis had previously been applied to its two components, i.e., hatching and fledging success.

Table 9 displays total reproductive success data for early and late started areas from 1977. Clutches in early started areas consistently fledged more than two chicks per nest (range: 2.09-2.50 chicks per nest) and when pooled, produced 2.20 chicks per nest. On the other hand, clutches in late started areas failed to produce more than one chick per nest (range: 0.72-0.96 chick per nest) and when pooled, produced 0.86 chick per nest.

Tables 10A and 10B display the seasonal trend in total reproductive success within early and late started study areas from 1977. When all clutch sizes were pooled or just 3-egg clutches considered, early, peak clutches produced more chicks per nest than early pre- or post-peak clutches. The seasonal relationship with total reproductive success was not so clear in late started study areas. When all clutch sizes were pooled, late pre-median clutches produced more chicks per nest than late post-median nests; however, when 3-egg clutches were considered, late post-median clutches produced more chicks per nest than late pre-median nests.

Table 11 displays the distribution of brood sizes at hatching and fledging for 3-egg clutches laid in early and late started areas from 1977. Of the 71 early started 3-chick broods at hatching, 47 (66.2%) were 3-chick

TABLE 9: Total reproductive success in early and late started areas from 1977

	Area Number	Clutches (n)	Chicks Fledged[1] (n)	Chicks Fledged Per Nest ± S.E.
Early Started Areas	1	23	49	2.13 ± 0.19
	2	20	42	2.10 ± 0.22
	3	33	69	2.09 ± 0.21
	4	14	35	2.50 ± 0.27
	5	23	54	2.35 ± 0.16
	Total	113	249	2.20 ± 0.09
Late Started Areas	6	18	13	0.72 ± 0.21
	7	24	23	0.96 ± 0.18
	Total	42	36	0.86 ± 0.13

[1]Chicks were considered fledged if they survived to 30 days of age.

TABLE 10A: Seasonal trend in total reproductive success within early started areas from 1977

Date Clutches Initiated	Clutches (n)	Chicks Fledged (n)	Chicks Fledged Per Nest ± S.E.
All Clutch Sizes			
9-22 April Pre-peak	23	49	2.13 ± 0.20
23-30 April Peak	73	169	2.32 ± 0.11
1 May-1 June Post-peak	17	31	1.82 ± 0.29
3-Egg Clutches			
9-22 April Pre-peak	18	35	1.94 ± 0.22
23-30 April Peak	66	157	2.38 ± 0.11
1 May-1 June Post-peak	13	24	1.85 ± 0.30

TABLE 10B: Seasonal trend in total reproductive success within late started areas from 1977

Date Clutches Initiated	Clutches (n)	Chicks Fledged (n)	Chicks Fledged Per Nest ± S.E.
All Clutch Sizes			
2-18 May Pre-median	21	25	1.19 ± 0.19
19 May-14 June Post-median	21	11	0.52 ± 0.16
3-Egg Clutches			
2-18 May Pre-median	17	18	1.06 ± 0.22
19 May-14 June Post-median	8	10	1.25 ± 0.25

TABLE 11: The distribution of brood sizes at hatching and fledging for 3-egg clutches in early and late started areas from 1977

	Brood Size At Hatching				Brood Size At Fledging			
	0	1	2	3	0	1	2	3
	(n)				(n)			
Early Started Areas	4	5	17	71	8	9	33	47
Late Started Areas	3	6	6	10	7	8	10	0

broods at fledging. In contrast none of the 10 late started 3-chick broods at hatching were 3-chick broods at fledging. In fact no brood sizes larger than 2 chicks were fledged in late started study areas while three 4-chick broods were successfully fledged in early started areas.

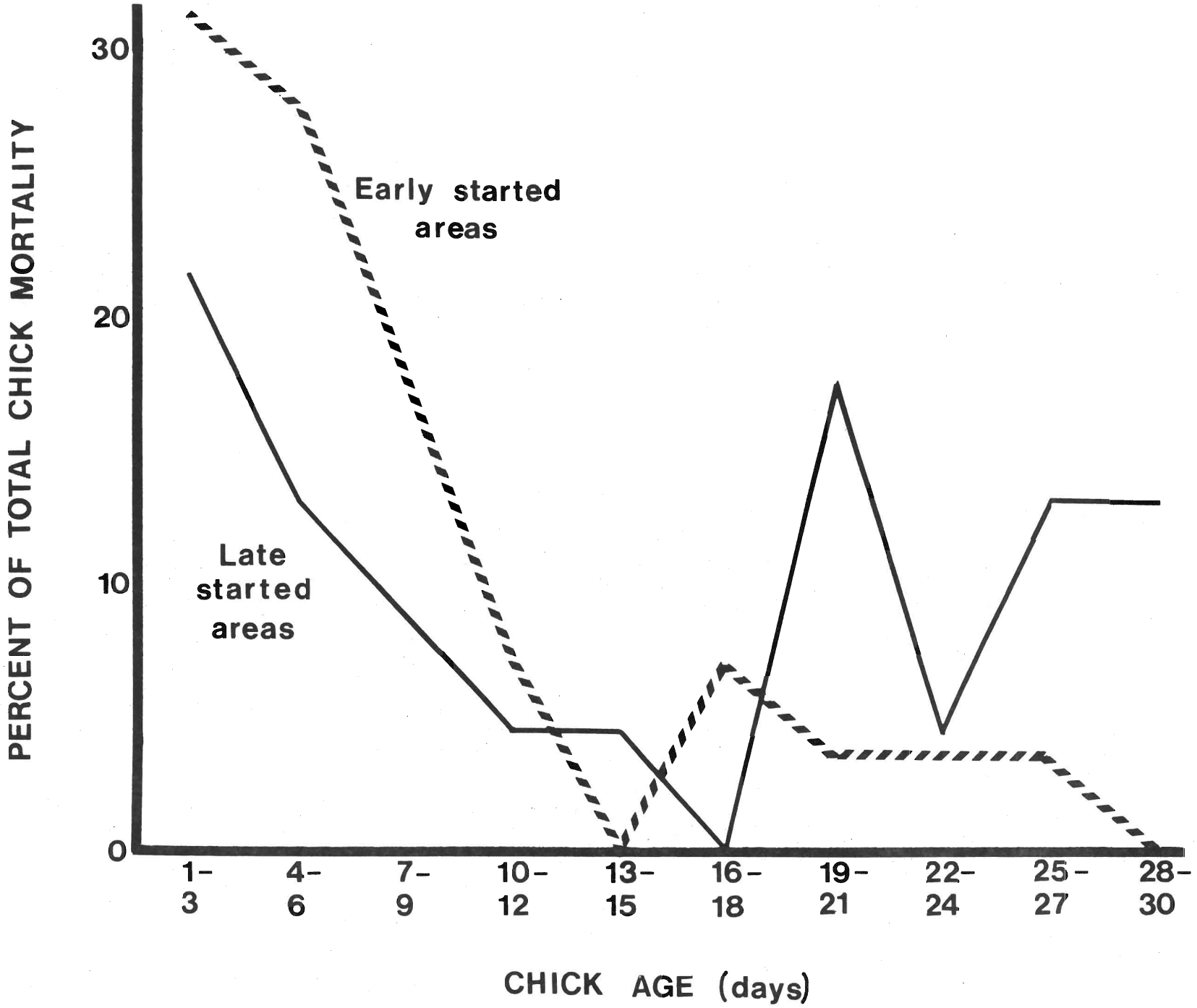
(e) Chick mortality

Figure 3 displays the relationship between the percent of total chick mortality (known dead) and chick age for early and late started areas from 1977. The sample size of disappeared chicks was low (early: n = 3; late: n = 3) for both clutch start times, therefore, this category of chick loss was not included in the analysis. The majority of chicks from early started nests died at an early age, while late started chick mortality was spread out over the entire fledging period, but concentrated during the first three days of life and from 19 to 21 days of age.

The fact that a substantial amount (13%, n = 3) of late started chick mortality occurred between 28 and 30 days of age suggests that fledging success data for late chicks (see Tables 7 and 8B) may be somewhat inflated due to a probable continuance of mortality subsequent to 30 days of age but prior to real fledging.

Due to the difficulty in discerning the causes of chick mortality, this topic was not studied in detail. Many dead chicks exhibited no external signs of trauma, while others showed obvious signs of being pecked. Whether this pecking was actually a cause of death is difficult to determine because on several occasions dead chicks were observed being 'molested' and pecked.

Figure 3: The relationship between percent of total chick mortality and chick age in early and late started areas from 1977.


PERCENT OF TOTAL CHICK MORTALITY
30
20
10
0
Early started areas
Late started areas
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
CHICK AGE (days)

The incidence of lameness or inability to fly as caused by broken bones, swollen or twisted joints, congenital abnormalities or other obvious factor was very low (n = 2) in both years of study in either early or late started areas.

(f) Chick growth

Certain standard procedures were adhered to when analysing chick growth. Inspection of growth curves of chicks from early and late started clutches revealed a linear relationship between chick weight and age from 5 to 20 days. Thus, when characterizing patterns of chick growth, only weights taken from chicks 5 to 20 days of age were used. Growth data were pooled into groups representing chicks from early pre-peak, early peak and late clutches. Only those broods containing the same number of chicks at hatching and fledging (30 days of age) were used, and seasonal comparisons of chick growth were only made between groups of chicks from broods of the same size. In broods where chick mortality occurred, only those where the chick(s) died before 6 days of age were used in the analysis.

Linear regression analysis was used to fit lines defining the relationship between weight and age for each pooled group of chicks (Figures 4A, 4B, and 4C). Although the resultant regression equations provided estimates of chick growth rate (slope) and elevation, statistical comparisons between regression lines could not be made due to the lack of independence of data points forming each regression line.

Due to low sample sizes of certain brood sizes, seasonal comparisons of chick growth could only be made with groups of chicks in 2- and 3-chick broods.

Figure 4A: Regression lines fitting the relationship between chick weight and age from 5 to 20 days for early started pre-peak and peak 3-chick broods.

A: Peak, 3-chick broods,
n = 26 chicks, weight = 22.12 (age) - 19.13

B: Pre-peak, 3-chick broods,
n = 42 chicks, weight = 22.47 (age) - 28.52

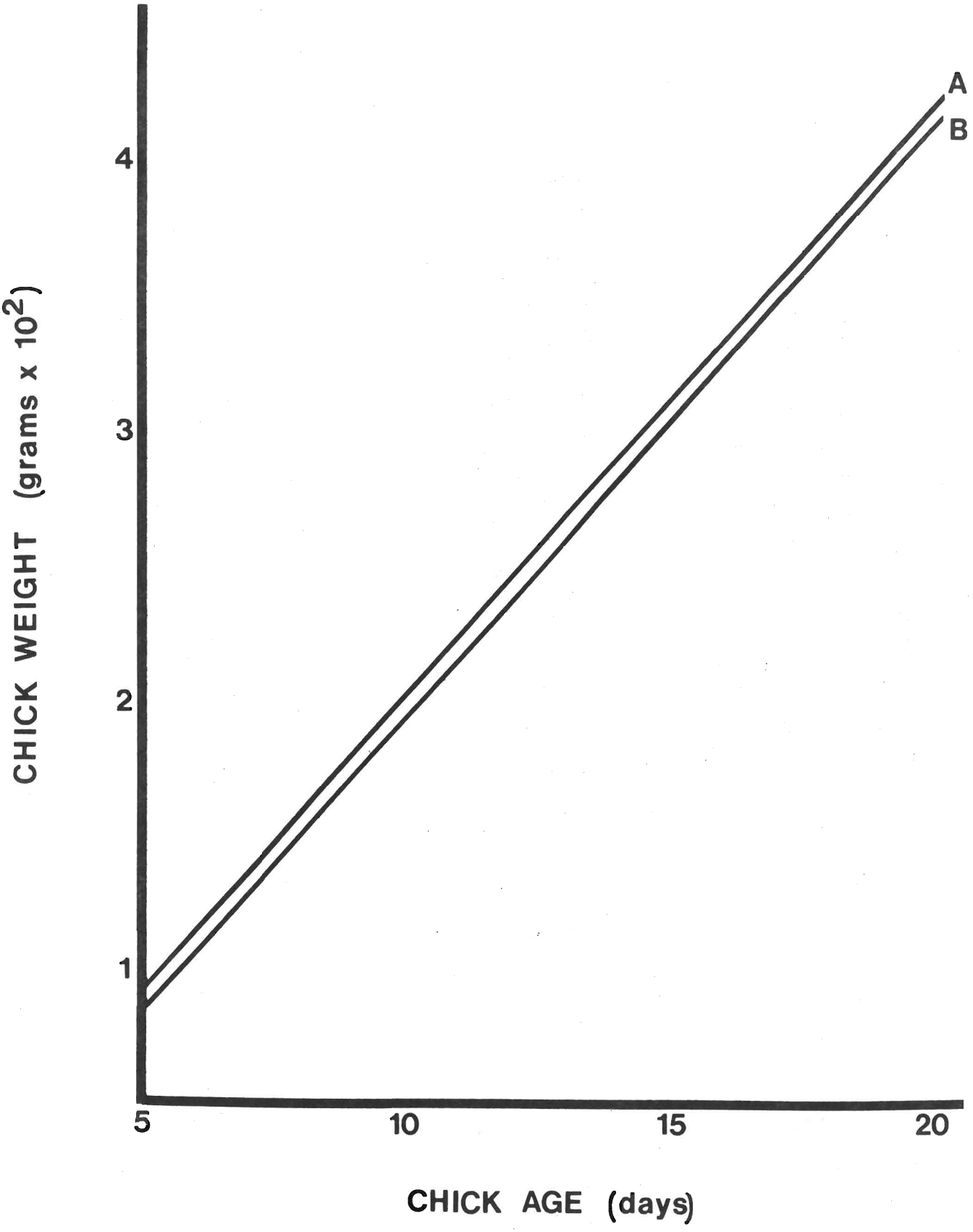

A
B
4
3
2
1
CHICK WEIGHT (grams x 10^2)
5
10
15
20
CHICK AGE (days)

Figure 4B: Regression lines fitting the relationship between chick weight and age from 5 to 20 days for early started pre-peak, early started peak, and late started 2-chick broods.

A: Pre-peak, 2-chick broods,
n = 24 chicks, weight = 22.02 (age) - 15.13

B: Peak, 2-chick broods,
n = 16 chicks, weight = 20.27 (age) - 8.85

C: Late, 2-chick broods,
n = 16 chicks, weight = 18.35 (age) - 11.14

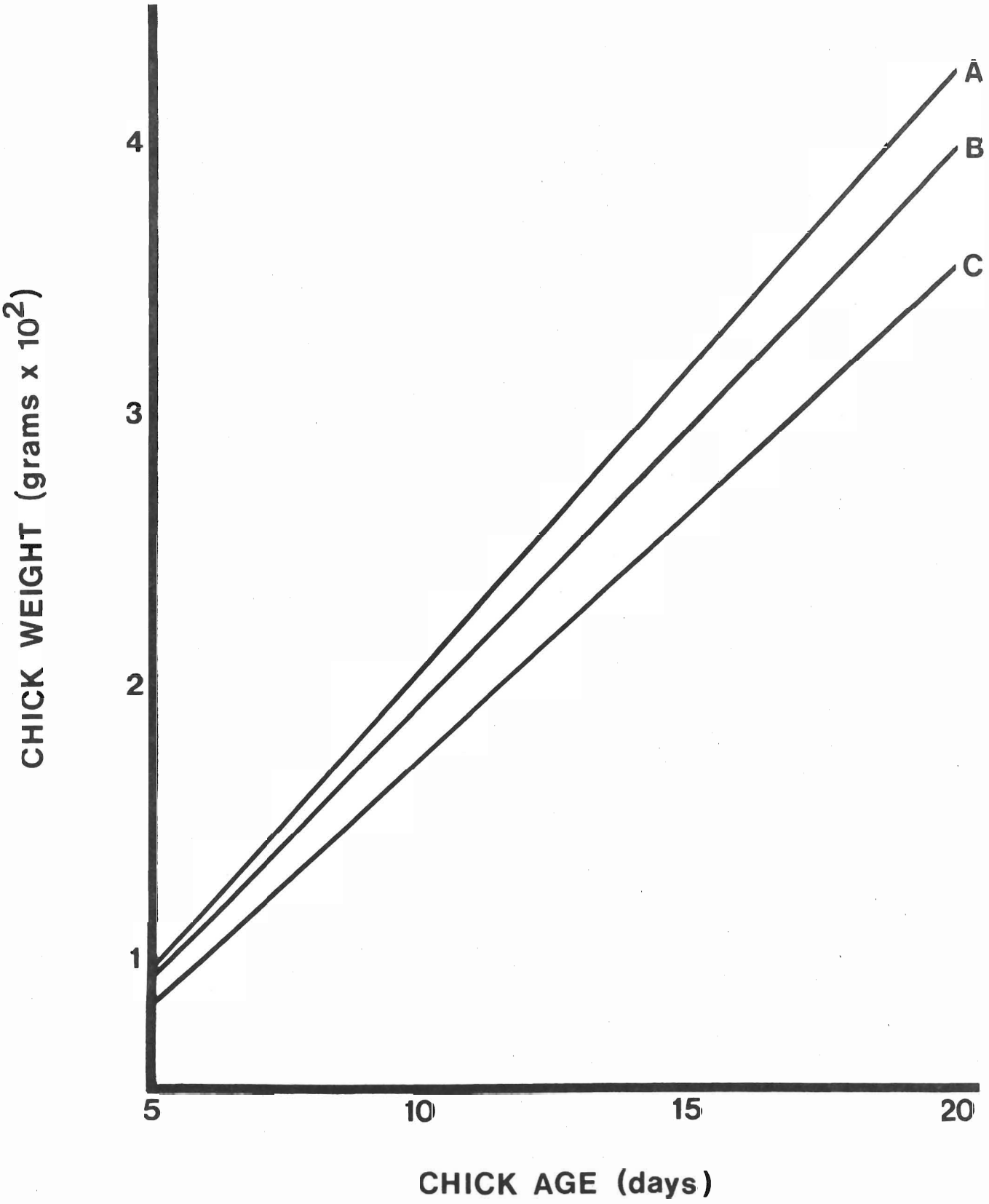
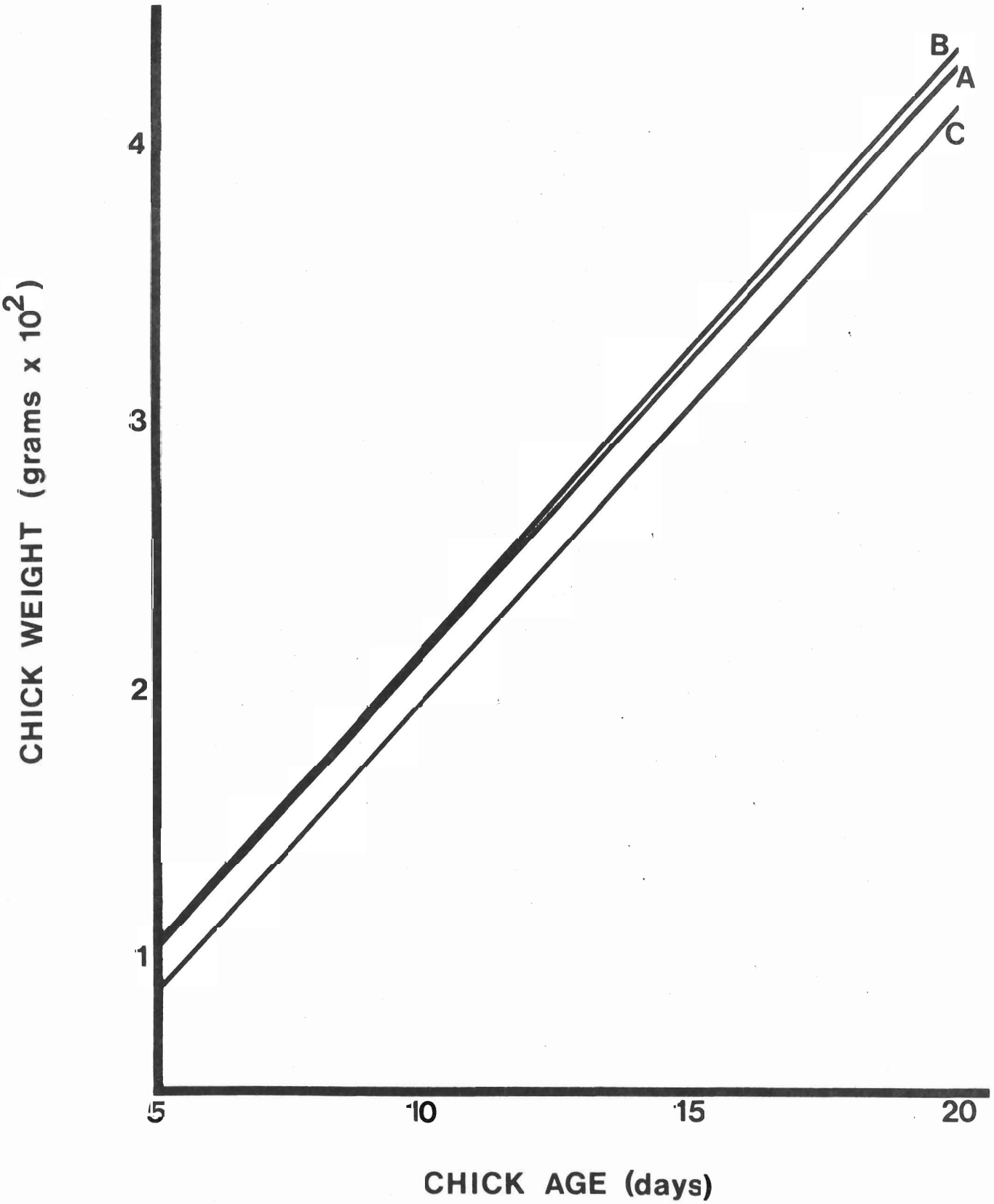

A
B
C
4
3
2
1
5
10
15
20
CHICK WEIGHT (grams x 10^2)
CHICK AGE (days)

Figure 4C: Regression lines fitting the relationship between chick weight and age from 5 to 20 days for A-, B-, and C-chicks in early started pre-peak and peak 3-chick broods.

A: A-chicks in early, 3-chick broods,
n = 7 chicks, weight = 19.80 (age) + 7.13

B: B-chicks in early, 3-chick broods,
n = 7 chicks, weight = 22.28 (age) -10.72

C: C-chicks in early, 3-chick broods,
n = 7 chicks, weight = 21.97 (age) -21.74


B
A
C
4
3
2
1
5
10
15
20
CHICK WEIGHT (grams x 10^2)
CHICK AGE (days)

The rate and elevation of growth of chicks in 3-chick broods from pre-peak and peak clutches was virtually identical (Figure 4A). On average, chicks from these clutches grew at the rate of approximately 22 grams per day, from 5 to 20 days of age. Some seasonal differences in the growth of chicks in 2-chick broods were found (Figure 4B). Chicks in late 2-chick broods experienced a lower rate of growth (approximately 18 grams per day) than chicks in 2-chick broods from pre-peak or peak clutches. Chicks in 2-chick broods from pre-peak clutches experienced approximately the same rate and elevation of growth as their 3-chick brood counterparts from pre-peak or peak clutches. Chicks in 2-chick broods from peak clutches grew at a slightly lower rate (approximately 20 grams per day) than their pre-peak counterparts or chicks in 3-chick broods from either pre-peak or peak clutches.

Seasonal trends in intra-brood growth differences could not be studied in detail due to the lack of 3-chick broods in late started study areas. Figure 4C displays the only intra-brood chick growth analysis performed; that of 3-chick broods from pre-peak and peak 3-egg clutches where the complete hatching order of the chicks was known. Only 7 broods could be used for analysis. The growth rates of A-, B- and C-chicks (from eggs-1, -2 and -3, respectively) were very similar and averaged approximately 21-22 grams per day from age 5 to 20 days. The elevation of the growth lines was similar in A- and B-chicks while the elevation of the C-chick's growth line was below that of the A- or B-chick.

(g) Chick hatching and fledging weights

Intra-brood and seasonal trends in chick hatching weights were investigated in order to determine whether this factor correlated with intra-brood and seasonal trends in chick growth and survival to fledging. Only 3-egg clutches hatching 3 eggs where at least the hatching order of egg-3 was known, were used in this analysis. Mann-Whitney U tests revealed various differences in chick group comparisons.

Intra-brood comparisons of hatching weights of A- and B-chicks from either early started peak or late clutches showed no statistically significant differences (Peak: $U = 37$, $n_1 = 9$, $n_2 = 9$, $p > 0.10$; Late: $U = 11.5$, $n_1 = 5$, $n_2 = 7$, $p = 0.39$). Thus, for subsequent intra-brood and seasonal comparisons, the hatching weights of A- and B-chicks were pooled. Wherever possible, the hatching weights of chicks known to be either A- or B-chicks were pooled with known A- and B-chicks.

The hatching weights of C-chicks were significantly lower than those for the pooled group of A- and B-chicks in both early started peak clutches ($z = 2.41$, $n_1 = 13$, $n_2 = 28$, $p = 0.016$) and late started clutches ($U = 15$, $n_1 = 7$, $n_2 = 12$, $p < 0.05$). When early started pre-peak clutches were pooled with the above sample of early started peak clutches, C-chicks still weighed significantly less at hatching than A- and B-chicks ($z = 2.73$, $n_1 = 19$, $n_2 = 40$, $p = 0.006$).

Seasonal comparisons of chick hatching weights revealed no significant differences between pre-peak, peak and late groups of chicks when hatching order was standardized in each comparison (Mann-Whitney U tests, $p > 0.10$).

Chicks were weighed only once, on or after 30 days of age. Thus, a weight at 30 days or some short time after, was in many cases not available (and not

TABLE 12: Distribution of fledging weights of chicks in 2-chick broods in early and late started areas from 1977

	Clutch initiation Period	Fledging Weight[1] <400 grams chicks[2] (n)	Fledging Weight[1] ≥400 grams chicks[2] (n)
Early Started Areas	pre-peak	0	14
	peak	3	17
	Total	3	31
Late Started Areas	Total	7	10

[1]Last chick weight taken on or after 30 days of age

[2]Chicks in 2-chick broods from hatching to fledging

easily estimated) for the chicks studied in the previous hatching weight analysis. However, Table 12 displays a crude attempt to compare fledging weights seasonally, while keeping brood size constant. Only 2-chick broods remaining that way from hatching to fledging (cf. Figure 4B) were used in this analysis. The last time a chick was weighed, on or after 30 days of age, was considered its fledging weight. A more discreet analysis of the data revealed that the majority of chicks from pre-peak, peak and late nests fledged at a weight somewhere between 400 and 500 grams. A comparison of the proportion of pre-peak and peak fledging weights over 400 grams to those 399 grams or under revealed no significant difference ($p = 0.19$, Fisher Exact Probability Test). When pre-peak and peak fledging weights were pooled and compared to late fledging weights, a significantly higher proportion of late chicks fledged at weights less than 400 grams ($\chi^2_c = 5.61$, $p < 0.025$).

V: The relationship between clutch size and reproductive success of Ring-billed Gulls nesting on Gull Island in 1976 and 1977

Data in (IV) above, were reorganized in Tables 13A (1976) and 13B (1977) to investigate the relationship between clutch size and hatching, fledging and total reproductive success. This analysis involved comparing the reproductive success of different clutch sizes within early and late started areas and the same clutch sizes between early and late started areas. Due to low sample sizes, the analysis was limited to 1, 2, 3, and 4-egg clutches.

(a) Hatching success

Generally, 3-egg clutches hatched with a higher success than other clutch sizes in both years of study (Tables 13A and 13B). In 1976, 3-egg clutches hatched significantly better than 2-egg clutches in both early

Table 13A: The relationship between clutch size and hatching success in early and late started areas from 1976

	Clutch Size	Clutches (n)	Eggs Laid (n)	Eggs Hatched (n)	Hatch/ Lay
Early Started Areas	3	140	420	385	0.92
	2	10	20	15	0.75
Late Started Areas	3	24	72	61	0.85
	2	10	20	10	0.50

Table 13B: The relationship between clutch size and reproductive success in early and late started areas from 1977.

	Clutch Size	Clutches (n)	Eggs Laid (n)	Eggs Hatched (n)	Chicks (n)	Hatch/Lay	Fledge/Hatch	Mean Fledge/ Nest ± SE
Early Started Areas	4	9	36	27	26	0.75	0.96	2.89 ± 0.31
	3	97	291	252	216	0.87	0.86	2.23 ± 0.09
	2	5	10	5	5	0.50	1.00	1.00 ± 0.45
Late Started Areas	3	25	75	48	28	0.64	0.58	1.12 ± 0.17
	2	10	20	13	6	0.65	0.46	0.60 ± 0.27
	1	5	5	1	0	0.20	0.0	0.0

started (χ^2_c = 4.56, $p < 0.05$) and late started (χ^2_c = 8.77, $p < 0.005$) areas (Table 13A). In 1977, 3-egg clutches again hatched significantly better than 2-egg clutches but only in early started study areas (χ^2_c = 7.65, $p < 0.01$) (Table 13B). In late started study areas, the hatching success of 2- and 3-egg clutches was similar (χ^2_c = 0.032, $p > 0.75$). One-egg clutches laid in late started study areas from 1977 hatched with a lower success than either 2- or 3-egg clutches laid in that same time period; however, the differences were both non-significant (3 vs 1-egg clutches: χ^2_c = 2.19, $p > 0.01$; 2 vs 1-egg clutches: χ^2_c = 1.72, $p > 0.10$) (Table 13B). The hatching success of 4-egg clutches laid in the early started study areas from 1977 was intermediate between 3- and 2-egg clutches laid in that time period; however, the differences were again non-significant (4 vs 3-egg clutches: χ^2_c = 2.58, $p > 0.10$; 4 vs 2-egg clutches: χ^2_c = 1.28, $p > 0.25$) (Table 13B).

In both years of study, early 3-egg clutches hatched with a significantly higher success than their late started counterparts (1976: χ^2_c = 2.73, $0.05 < p < 0.10$; 1977: χ^2_c = 19.10, $p < 0.005$). No clear seasonal trend was observed in the hatching success of 2-egg clutches, over both study years. In 1976, early 2-egg clutches hatched with a higher success than their late started counterparts, while in 1977, late 2-egg clutches hatched with a higher success than their early started counterparts. χ^2_c tests revealed no significant differences in the above 2-egg clutch comparisons.

Approximately half of all egg failure occurring in either 2- or 3-egg clutches was loss due to addling. Relationships between clutch size and causes of egg loss were not obvious. Eggs in 2-egg clutches tended to be predated and deserted more often than eggs in 3-egg clutches.

(b) Fledging success

No clear trends in the relationship between clutch size and fledging success were evident (Table 13B). In early started areas from 1977, chicks from 3-egg clutches fledged with poorer success than either chicks from 2- or 4-egg clutches, although the only testable comparison was not statistically significant (3 vs 4-egg clutches: $\chi^2_c = 1.54$, $p > 0.10$). In late started areas from 1977, chicks from 3-egg clutches fledged more successfully than chicks from 2-egg clutches although the difference was not significant ($\chi^2_c = 0.23$, $p > 0.50$). One-egg clutches were unsuccessful in fledging any chicks.

Chicks from either 2- or 3-egg clutches in early started areas fledged with a significantly higher success than their late started counterparts (2-egg clutches: $p = 0.05$, Fisher Exact Probability Test; 3-egg clutches: $\chi^2_c = 18.15$, $p < 0.005$).

(c) Total reproductive success

In general, there was a direct relationship between clutch size and total reproductive success expressed as number of chicks fledged per nest (Table 13B). Four-egg clutches produced more chicks (2.89) than any other clutch size. Early started 3-egg clutches were next most successful and produced 2.23 chicks/nest, followed by late started 3-egg clutches that produced 1.12 chicks/nest. Early started 2-egg clutches produced 1.00 chick/nest while their late started counterparts produced only 0.60 chick/nest. Late started 1-egg clutches were reproductively unsuccessful and produced no chicks per nest.

VI: The relationship between laying order and reproductive success

Table 14 displays the relationship between laying order and reproductive success of 3-egg clutches laid in early and late started study areas from 1977. Hatching success data from 1976 was not considered due to the low sample size of 3-egg clutches with known laying and hatching order.

It should be noted that the early started sample in this analysis is biased in that it does not fairly represent 3-egg clutches that hatched over a relatively short period of time (i.e., 0 or 1 day). The hatching order of eggs in these clutches was generally unknown and thus they could not be used in this analysis.

(a) Hatching success

The hatching success of eggs-1, 2 and 3 in early started areas was virtually identical. Eggs-1 and 2 hatched with exactly the same success while egg-3 hatched with a slightly higher success. The hatching success in late started 3-egg clutches decreased with the order of laying but the differences were not statistically significant (χ^2 tests, $p > 0.10$).

Table 14: The relationship between laying order and reproductive success in early and late started areas from 1977.

	Laying Order	Eggs Hatched (n)	Chicks Fledged (n)	Hatch/Lay	Fledge/Hatch	Fledge/Lay
Early Started Areas (clutches[1] (n) = 44)	1	35	33	0.80	0.94	0.75
	2	35	29	0.80	0.83	0.66
	3	36	27	0.82	0.75	0.61
Late Started Areas (clutches[1] (n) = 21)	1	16	11	0.76	0.69	0.52
	2	14	9	0.67	0.64	0.43
	3	13	4	0.62	0.31	0.19

[1]Only those 3-egg clutches where laying and hatching order known were considered.

(b) Fledging success

Fledging success decreased with laying order in both early and late started areas; however, this decrease was more dramatic in the late started areas (Table 14). A-chicks fledged with higher success than B-chicks in both early and late started areas but neither comparison was significant (χ^2_c tests, $p > 0.10$). C-chicks fledged with poorer success than either A- or B-chicks in both early and late started areas. Fledging success comparisons between the C-chick and the A- or B-chick were either marginally significant (A vs C-chick: $\chi^2_c = 3.68$, $0.05 < p < 0.10$) or non-significant (B- vs C-chick: $\chi^2_c = 0.27$, $p > 0.50$) in early started areas and either significant (A- vs C-chick: $p = 0.048$, Fisher Exact Probability Test) or marginally significant (B- vs C-chick: $p = 0.087$, Fisher Exact Probability Test) in late started areas.

(c) Total reproductive success

An analysis of total reproductive success, expressed in Table 14 as Fledge/Lay (chicks fledged per egg laid) revealed that there were no significant differences in the reproductive success of eggs 1, 2 or 3 (χ^2_c Tests $p > 0.10$) in early started areas. In late started areas, the total reproductive success of egg-3 was significantly lower than egg-1 ($p = 0.026$, Fisher Exact Probability Test) and marginally lower than egg-2 ($p = 0.091$ Fisher Exact Probability Test).

SECTION 2: The relationships between the date of clutch initiation and certain aspects of the reproductive biology of the Ring-billed Gull nesting on Gull Island in 1977

I: Incubation period

The incubation period of a clutch is defined, in this thesis, as the number of days the last laid egg in a clutch takes to hatch, based on daily visits to the colony.

Figure 5 displays the relationship between the date of clutch completion and incubation period for 3-egg clutches hatching at least the third laid egg, from early and late started areas. An inverse, curvilinear relationship was fitted between incubation period and the date of clutch completion in early clutches using curvilinear regression analysis. The incubation period of individual clutches ranged from a high of 33 days to a low of 23 days.

No such relationship obtained in late started nests. The incubation period of individual nests stayed relatively constant in this time period and ranged from 23 to 26 days with a mean of 24.7 days.

II: Hatching period

Hatching period, in this thesis, is defined as the time between the hatching of the first and last eggs in a clutch, based on daily visits to the colony.

While in the 1977 field season, it was noticed that considerable variability in hatching period existed within the early nest start distribution and between the early and late nest start distributions. Some clutches hatched between visits to the colony (Hatch period = 0 days) while others hatched

Figure 5: The relationship between incubation period[1] and date of clutch completion in early and late started areas from 1977.

1. Time to hatch of the last laid egg in 3-egg clutches where at least the hatching order of that egg is known.

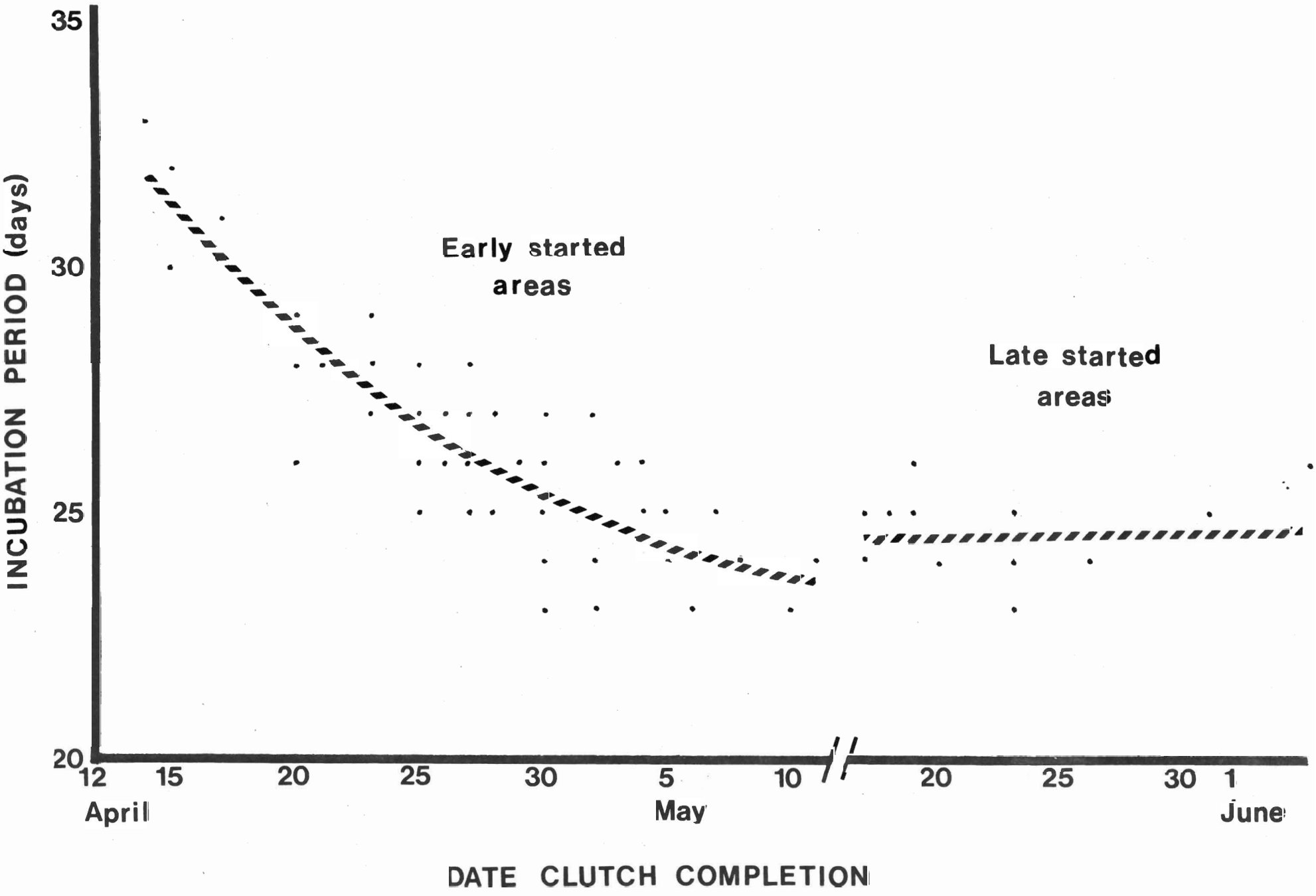

35
30
25
20
INCUBATION PERIOD (days)
Early started areas
Late started areas
12
15
20
25
30
5
10
20
25
30
1
April
May
June
DATE CLUTCH COMPLETION

Table 15: Distribution of hatching periods for early and late started areas from 1977.

	Hatching Period (days) Clutches[1] (n)						Proportion Asynchronous of total clutches
	Synchronous		Asynchronous				
	0	1	2	3	4	5	
Early Started Areas	12	38	9	7	0	0	0.24
Late Started Areas	0	1	1	5	2	1	0.90

[1]3-egg clutches hatching 3 eggs

Table 16: Distribution of laying periods for early and late started areas from 1977

	Laying Period (days) Clutches[1] (n)											
	Between Eggs 1-2			2-3					1-3			
	1	2	3	1	2	3	4	5	3	4	5	6
Early startes areas	7	47	12	6	52	6	1	1	8	42	14	2
Late started areas	0	9	1	1	9	0	0	0	1	8	1	0

[1]3-egg clutches hatching 3 eggs

over longer periods of time (maximum hatch period = 5 days). Clutches were categorized into synchronous (hatch period $\leq$ 1 day) and asynchronous (hatch period $\geq$ 2 days) groups.

Table 15 displays the distribution of hatch periods and the proportion of asynchronous hatching clutches, for 3-egg clutches hatching 3 eggs in early and late started areas from 1977. Most (n = 50, 76%) early started clutches were classed as synchronous, the modal hatch period being 1 day. On the other hand, most (n = 9, 90%) late started clutches were classed as asynchronous, the modal hatch period being 3 days. The difference in the proportion of asynchronous and synchronous hatching clutches occurring in early and late started areas was significant (χ^2_c = 14.2, $p < 0.001$). This difference may not be surprising if the laying period (time between the laying of the first and last eggs in a clutch) differed between early and late started areas in the same way. However, an analysis of the laying period data (Table 16) showed that no significant differences occurred between early and late started areas (Mann-Whitney U Test for large samples, $z = 0.49$, $n_1 = 10$, $n_2 = 66$, $p = 0.62$). The majority of 3-egg clutches hatching 3 eggs were laid over a 4-day period in both early and late started study areas; two days separating the laying of eggs-1 and 2 and eggs-2 and 3, in most cases.

Due to some temporal overlap between early and late clutch start distributions, it was decided to reorganize the hatching period data in order to determine when the 16 early, asynchronous clutches (Table 15) were initiated in early started areas. The expected result was that since asynchronous hatching seemed to be a phenomenon associated with clutches laid in late started areas, a higher proportion of asynchronous hatching clutches would be initiated in the later part of the early clutch start distribution. Table

Table 17: Distribution of synchronous and asynchronous hatching clutches according to date of clutch initiation within early started areas from 1977.

Clutches[1] initiated	Synchronous (n)	Asynchronous (n)
9-28 April	44	8
29 April-1 June	6	8

[1]3-egg clutches hatching 3 eggs.

17 displays the results of this analysis and indicates that the above expectation was borne out by the data. A χ_c^2 test was used to determine a date of clutch initiation subsequent to which, the proportion of asynchronous hatching clutches was significantly greater than the proportion prior to the date chosen. It was found that a significantly higher proportion of asynchronous hatching clutches were produced after 28 April in early started areas ($\chi_c^2 = 8.32$, $p < 0.005$). Again, this difference was not due to laying period differences before and after 28 April (Mann-Whitney U Test for large samples, $z = 0.36$, $n_1 = 14$, $n_2 = 52$, $p = 0.72$).

SECTION 3: The incubation attentiveness of Ring-billed Gulls nesting on Gull Island in 1977

In the following analysis of various aspects of Ring-billed Gull incubation attentiveness, certain standard analytical procedures were adhered to. Sample sizes of the various clutch sizes monitored, allowed only 3-egg clutches to be considered. Furthermore, only those 3-egg clutches hatching 3 eggs were used in the analysis. Data from individual pairs of gulls were pooled according to the time of clutch initiation, in order to study seasonal trends in incubation attentiveness. Every effort was made to reduce the time span of clutch initiation within these groups. The diel period was divided into 'day' or diurnal period from 0600 to 1800 hours and 'night' or nocturnal period from 1800 to 0600 hours, EST.

Five 3-egg clutches initiated on 18, 19 or 20 April were chosen as representative of the pre-peak period of the early clutch start distribution, and seven 3-egg clutches initiated on 27 or 28 April were chosen as representative of the peak period of the early clutch start distribution (cf. Figure 2A). Six 3-egg clutches initiated between 12 and 19 May were chosen as representative of the late clutch start distribution (cf. Figure 2B).

The reproductive success of 10, monitored 3-egg clutches initiated between 25 and 28 April in study area 3 was compared to 25 unmonitored 3-egg clutches initiated during the same time period in the same study area. The results of the analysis are displayed in Table 18. No significant differences

Table 18: The relationship between the monitoring of incubation attentiveness and reproductive success.

	Eggs Laid (n)	Eggs Hatched (n)	Chicks Fledged (n)	Hatch/Lay	Fledge/Hatch	Fledge/Lay
Monitored clutches[1]	30	27	22	0.90	0.82	0.73
Unmonitored clutches[1]	75	68	65	0.91	0.96	0.87

[1]3-egg clutches initiated between 25-28 April in study area 3.

were observed in either the hatching success or total reproductive success of monitored or unmonitored clutches (χ^2_c tests, $p > 0.10$). Fledging success was marginally lower in monitored clutches than in unmonitored nests ($\chi^2_c = 3.32$, $0.05 < p < 0.10$).

There was no reason to suspect that the monitoring devices significantly affected incubation behaviour. On many occasions Ring-billed Gulls were observed to return to monitored clutches, never having seen or experienced the monitoring device before, and commence incubation within as little as 10-20 minutes.

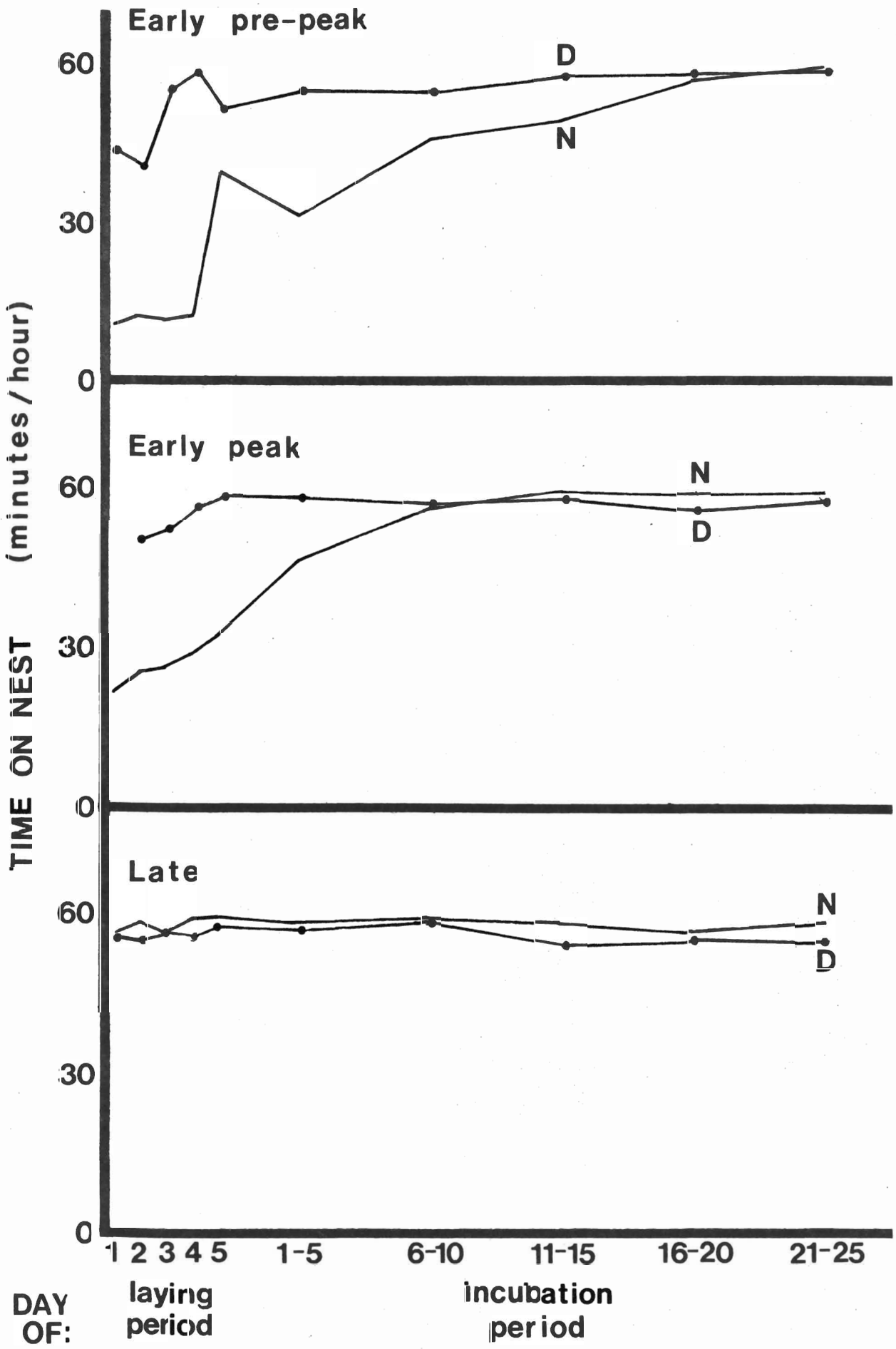
I: Seasonal trends in incubation patterns

Diurnal and nocturnal incubation attentiveness patterns over the egg laying period (Day 1-5) and the incubation period proper (Day 1-25), for the samples of early pre-peak and peak and late started clutches are in Figure 6. Day-to-day incubation attentiveness during the incubation period, was similar enough to warrant the pooling of data over 5-day time blocks in order to 'smooth out' the incubation pattern.

A general increase in diurnal incubation attentiveness occurred between the laying of the first and third eggs in early clutches (Figure 6). No such increase in incubation attentiveness occurred during the egg-laying period of late clutches. The sample size of hours analysed during the egg-laying period was small and it is thus difficult to say whether the above differences were significant. In any case, diurnal incubation attentiveness during the egg-laying period did not drop below 50 mins/hour in the early clutches monitored. Diurnal incubation attentiveness during the incubation period was constantly high (range for 5-day time block means 57.5-59.5 mins/hour) in early pre-peak, peak and late clutches.

Figure 6: Patterns of incubation attentiveness[1] for early started pre-peak, early started peak and late started clutches.[2]

1. Time on nest (minutes per hour) versus day in laying and incubation period for: Diurnal (D) period: 0600-1800 (EST)
   Nocturnal (N) period: 1800-0600 (EST)
2. 3-egg clutches hatching three eggs


Early pre-peak
60
30
0
D
N
Early peak
60
30
0
N
D
Late
60
30
0
N
D
TIME ON NEST (minutes/hour)
1 2 3 4 5
1-5
6-10
11-15
16-20
21-25
DAY OF:
laying period
incubation period

No consistent trend in diurnal incubation attentiveness over the incubation period was observed.

Seasonal differences in incubation attentiveness were evident when the nocturnal period was considered (Figure 6). In the egg-laying period, nocturnal incubation attentiveness ranged from 10.8 to 39.3 mins/hour in pre-peak clutches and from 21.9 to 32.5 mins/hour in peak clutches. In the egg-laying period of late clutches, nocturnal incubation attentiveness was similar to diurnal levels and ranged from 57.4 to 59.2 mins/hour.

An increasing trend in nocturnal incubation attentiveness over the incubation period, was observed in early pre-peak and peak clutches. Early pre-peak clutches did not attain diurnal attentiveness levels during the nocturnal period, until the last 10 days of the incubation period. Early peak clutches, on the other hand, experienced depressed nocturnal attentiveness levels only during the first 5 days of the incubation period and thereafter incubated at diurnal levels.

II: Nocturnal desertion

(a) Description

Incubation attentiveness data showed depressed nocturnal levels in early started areas. This depression was caused by a behaviour characterized by the en mass exodus of Ring-billed Gulls from the Gull Island colony in the evening, and return in the morning, that will henceforth be termed nocturnal desertion.

The following description of nocturnal desertion is based on visual observations made from shore on 20 and 21 April 1977 at 1930 hours and 1900 hours respectively, and incubation attentiveness data from the event recorders. Appendix 1 summarizes nocturnal desertion data from early started areas 1, 2, and 3.

Nocturnal desertion occurred from the first monitored night (15 April) until 10 May at which point the behaviour was never observed again. In all probability, the behaviour occurred on most nights prior to 15 April (P. Fetterholf, pers. comm.). The first night the monitored gulls were known to stay on the colony occurred on 22 April and coincided with high winds and rain. Nocturnal desertion again did not occur in monitored areas on 1 May, a night also coinciding with high winds and rain. Subsequent to 1 May nocturnal desertion became less frequent toward 10 May.

Most (86-93% depending on study area considered) of the nocturnal desertions occurring before 4 May were participated in by all monitored birds and observations from shore suggested that it was a colony wide phenomenon. Subsequent to 4 May, from 50-100% (depending on study area considered) of the nocturnal desertions were participated in by fewer than 100% of the birds monitored. Desertion and subsequent resumption of incubation were generally, highly synchronous events. However, this synchrony deteriorated toward 10 May (cf. standard error of on and off times -Appendix 1) with the last nocturnal desertions being the least synchronous.

The duration of nocturnal desertion per night also decreased toward 10 May. Nocturnal desertion and resumption of incubation before 22 April, coincided approximately with sunset and sunrise and ranged in duration from a mean of 9 hours 53 minutes to 9 hours 21 minutes depending on the study area considered. The gulls' first observed night on the colony (22 April) had a disruptive effect on the synchrony and duration of nocturnal desertion, as did the gulls' second observed night on the colony (1 May). The duration of nocturnal desertion after 22 April fluctuated widely but never reached the pre-22 April levels of approximately 9.5 hours. Generally, nocturnal desertions were shortened by the gulls' staying later in the evening, on the

colony, before deserting; although, return times in the morning grew earlier and thus acted to reduce the duration of nocturnal desertion to a certain extent. After the actual desertion, the gulls were observed to ' mill about', above Gull Island and offshore, in very large cohesive flocks. Approximately 30 minutes after the desertion, gulls were observed breaking away from these large glocks and flying south-east from Gull Island, out into Lake Ontario. At this time visual observations were difficult to make because of light levels, thus the gulls were located by sound. For approximately another 30 minutes, gulls were heard moving from Gull Island, south-east into Lake Ontario. At no time were gulls either seen or heard flying inland after desertion.

(b) The relationship between date of egg-laying and total duration of nocturnal desertion.

With reference to the early clutch start distribution from 1977 (Figure 2), clutch initiation spanned the entire period nocturnal desertion occurred (from beginning of season to 10 May). Thus, clutches initiated early in the early started areas, experienced many days (or hours) of nocturnal desertion before hatching occurred, while clutches initiated late in the early started areas experienced relatively few days (or hours) of nocturnal desertion before hatching occurred. There was, in fact, virtually a continuum of clutches initiated between 9 April and 10 May that experienced greater or lesser amounts of nocturnal desertion. It is this 'natural experiment' that will subsequently be used to study and relate seasonal changes in certain reproductive parameters observed within the early clutch start distribution.

Figure 7: The relationship between the total, estimated duration of nocturnal desertion experienced by a particular egg and the laying date of that egg.

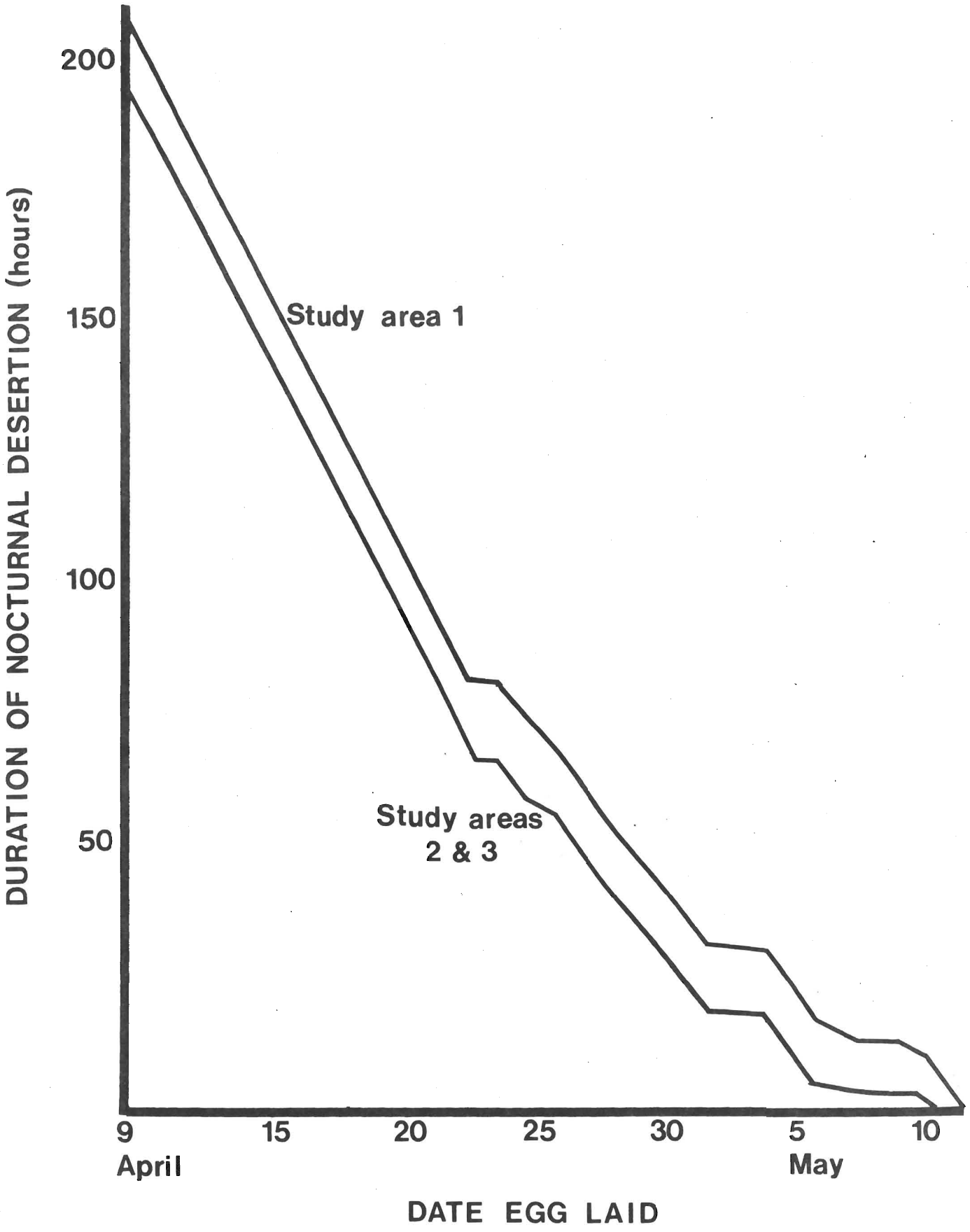

DURATION OF NOCTURNAL DESERTION (hours)
200
150
100
50
Study area 1
Study areas
2 & 3
9
April
15
20
25
30
5
May
10
DATE EGG LAID

Figure 7 shows the relationship between egg-laying date (regardless of laying order within a clutch) and the estimated total amount of nocturnal desertion (in hours) experienced by that egg from laying to hatching. This estimate was calculated from the mean duration of nocturnal desertion over all deserting birds, on a nightly basis, and within each study area. None of the eggs in the colony had hatched by 10 May (first egg hatched 15 May), thus there was no need to include the hatch date in the calculation of the estimated duration of nocturnal desertion experienced by a particular egg. Variability in this estimate between study areas 1 and 2, and, 1 and 3 warranted the calculation of a separate estimate for study area 1.

Estimates of the duration of nocturnal desertion for eggs laid prior to 15 April were based on the assumptions that (1) nocturnal desertion occurred consistently before 15 April, and (2) the nightly duration of nocturnal desertion prior to 15 April was approximated by the actual duration occurring on 15 April. A small source of error in the estimate of duration of nocturnal desertion was caused by the aforementioned observation that not all birds participated in the desertions after 4 May. Also, no incubation attentiveness data were obtained from study area 1 on 28-30 April and 1 May and from study area 2 on 28-30 April, thus an estimate of the duration of nocturnal desertion for the above dates, in those areas, was obtained from nocturnal desertion data from study area 3.

The results of this analysis (Figure 7) show that eggs laid during the pre-peak time period (9-22 April) experienced a total of approximately 80-200 hours of nocturnal desertion, before hatching. Peak (23-20 April) eggs experienced approximately 35-80 hours of nocturnal desertion while post-peak (1 May-1 June) eggs experienced approximately 0-25 hours.

DISCUSSION

Compared to Great Lakes Herring Gulls (Gilman et al., 1977; Morris and Haymes, 1977) and Common Terns (Morris et al., 1976), Gull Island Ring-billed Gulls reproduced very successfully in 1977. Early started clutches (comprising the majority of clutches on Gull Island in 1977), fledged an average of 2.20 chicks per nest (cf. Table 9). A mean clutch size of 3.04 together with high hatching (83%, n = 286) and fledging (87%, n = 249) success resulted in this level of reproductive output (cf. Tables 3A, 4 and 7).

Ludwig (1974) calculated that a reproductive success of 0.63 chicks per nest (pair) was required to maintain a stable Ring-billed Gull population in Lakes Michigan and Huron. Assuming that the parameters used by Ludwig to calculate this required reproductive success (post-fledge and annual adult mortality) are approximated in Lake Ontario, early nesting Ring-billed Gulls on Gull Island, in 1977, produced over three times the number of chicks required to maintain a stable population. Hatching success data from 1976 and estimates of fledging success from that year (not reported here) compare favourably with those for 1977 and suggest that the high reproductive success of early nesting Ring-billed Gulls in 1977 was not peculiar to that year. Thus, I suggest that in addition to other factors potentially responsible for the Great Lakes Ring-billed Gull population increase over at least the past 15 years (cf. Ludwig, 1974), high reproductive success may also have been a causative agent.

It should be noted that the various reproductive success data reported here are estimates that potentially were affected by a number of confounding factors. These can conveniently be grouped into those associated with

1. sampling error, and

2. observer effect.

With limited manpower resources available, less than 1% of all the Ring-billed Gull nests on Gull Island could be studied in any one year. Thus there was a possibility that the chosen study areas were not a representative sample of the total colony. However, this potential bias was reduced by locating study areas within the major habitat type on Gull Island (i.e., vegetated, soil substrate, no heterospecific breeding birds) where most of the Ring-billed Gulls were breeding. Casual observations indicated that the timing of clutch starts within the study areas and over the colony as a whole were similar.

With the level of investigator activity within the colony required to carry out a study such as this, I almost certainly had some effect on my study gulls. However, observer effect was reduced by spending only short periods of time (less than 1 hour) in any one study area. On only two instances was egg loss known to be directly associated with my activities (but cf. Robert and Ralph, 1975). Visual and event recorder data indicated that resumption of incubation behaviour was immediate upon my exit from a study area. My activities within the study areas caused older chicks to wander from their home territories and parents. However, the chicken wire fencing greatly reduced this effect by restricting chick movement. Certain effects of the fencing itself were noted during this study. Chicks often were found cut above the bill, presumably as a result of trying to escape the fenced area. Chicks and adults were on occasion found caught up in the chicken wire. Furthermore, fencing within a colony may prevent the natural expansion of the area used by each adult pair, upon the hatching of eggs

(P. Fetterholf, pers. comm.) Finally, Vermeer (1970) noted that fencing may protect chicks from natural predation. In summary, the effects of my presence in the Ring-billed Gull colony and any bias resulting from sampling error, although not quantified, are assumed to be small, as a result of precautions taken to minimize both factors.

This study has shown a direct relationship between clutch size (up to 4-egg clutches) and total reproductive success of Gull Island Ring-billed Gulls resulting in 4-egg clutches being the most productive in terms of chicks fledged per nest (cf. Table 13B). These results agree with those of Ward (1973) working on the Glaucous-winged Gull and support a theoretical model proposed by Charnov and Krebs (1974). These authors point out that Lack (1954) did not stress the factor of adult survival in his theory of the determination of clutch size in nidicolous birds. When it is assumed that adult mortality increases with clutch size, Charnov and Krebs' model predicts that the clutch size selected for will be smaller than that which simply "maximizes the number of young surviving to breed" (Lack's (1954) hypothesis). With respect to this study, the above model suggests that although here, 4-egg clutches were shown to be the most productive of all clutch sizes, 3-egg clutches have been selected for in the Ring-billed Gull, as a result of a balance between adult mortality and clutch size, maximizing an individual's fitness. An alternative hypothesis is that due to relatively recent increases in food availability (cf. Ludwig, 1974), the Ring-billed Gull is now able to fledge larger broods than it could in the past and thus 4-egg clutches are, at least at present, more productive than the commonest clutch size of three eggs (cf. Haymes and Morris, 1977).

Generally consistent with available larid literature, (e.g., Patterson, 1965; Brown, 1967; Kadlec and Drury, 1968; Parsons, 1975a) Gull Island Ring-

billed Gulls initiating clutches at the peak of clutch starts (23-30 April, cf. Figure 2A) produced more chicks per nest than counterparts initiating clutches either before or after these dates (cf. Tables 9 and 10A). Causes of this phenomenon were:

1. reduced hatching success of pre-peak compared to peak clutches (cf. Table 5A) which counteracted a higher mean clutch size (cf. Table 3B),
2. reduced mean clutch size and fledging success of post-peak compared to peak clutches (cf. Tables 3B and 8A), and
3. reduced mean clutch size, hatching success and fledging success of late compared to early clutches (cf. Tables 3A, 4 and 7).

These trends obtained when 3-egg clutches only were considered (with one exception: 1976 hatching success early vs late), indicating that they were not simply a function of differing clutch size distributions in each compared group of clutches.

No consistent trends in total reproductive success with date of clutch initiation were apparent in late started study areas from 1977 (cf. Table 10B). Decreases in mean clutch size and fledging success (cf. Tables 3B and 8B) resulted in lower total reproductive success in post-median clutches. However, when 3-egg clutches were considered, increased hatching success resulted in higher total reproductive success in post-median clutches. The possible cause(s) of these inconsistencies are unknown, but may be related to the arbitrary date at which the late clutches were divided to form the pre- and post-median groups.

Possible causes of the observed seasonal peak in the total reproductive success of Ring-billed Gulls breeding in early-started areas are many. The reduction in hatching success exhibited by pre-peak gulls was probably related to increased amounts of nocturnal desertion experienced by the eggs of these gulls, compared to eggs laid in either peak or post-peak time

periods. Pre-peak eggs experienced up to six times the duration of nocturnal desertion of peak eggs (cf. Figure 6). Furthermore, any deleterious effects of nocturnal desertion on hatching success may have been enhanced in pre-peak eggs by the generally lower ambient temperatures experienced during that part of the season. On at least two occasions, ground frost occurred during the pre-peak time period, which could have reduced the temperatures of deserted eggs below critical levels.

The deleterious effects of incubation interruption are well known in poultry science (e.g., Moreng and Bryant, 1956). These authors found an increase in the sensitivity of chicken embryos to 50-55°F (10-12.5°C) interruption temperatures with increasing embryo age, resulting in "a drastic reduction in hatchability" of eggs treated for periods lasting 19-120 hours, after the fourth day from egg laying. From Moreng and Bryant's work, I might have expected a more serious decrease in the hatching success of nocturnally deserted Ring-billed Gull eggs, than was the case. Recognizing differences in the regimes of incubation interruption between the laboratory study noted and nocturnally deserting Ring-billed Gulls, I suggest that data presented here indicate a low susceptibility to incubation interruption in the Ring-billed Gull. This is supported by Hunter et al. (1976) who found only small reductions in the hatching success of Ring-billed Gull eggs (as compared to appropriate field controls) experiencing from 4-12 hours of total incubation interruption (at 10°C) at various times throughout their incubation period.

Several factors were potentially responsible for the reduction in mean clutch size and hatching success in late clutches and fledging success in post-peak and late clutches. The majority (74%, n = 31) of Ring-billed Gull pairs nesting in late-started study areas, in 1977, contained at least one

immature plumaged parent (cf. Table 2). I suggest that this was at least one factor causing the lower mean clutch size, hatching success and fledging success in late-started areas. This contention is supported by many authors who have studied the effects of parental age or breeding experience, on the breeding biology of a variety of Larid species (e.g., Coulson and White, 1958, 1961; Coulson, 1966; Ryder, 1975; Haymes and Blokpoel, 1978).

The reasons for the lower total reproductive success of young breeding gulls are unknown (Ryder, 1975). Indeed, there are many untested hypotheses regarding this subject. A common suggestion is that young gulls are inexperienced breeders and thus not as able to care for their eggs and/or young as older, presumably more experienced, gulls. My findings indicate that the sample of event recorder-monitored Ring-billed Gulls nesting in late started areas (4 out of the 6 pairs in sample contained at least one immature gull) incubated their eggs as well as a sample of early counterparts (cf. Figure 6). The increased rate of egg loss due to cracking, rolling from nest and disappearance observed in late compared to early started areas in both study years could be accounted for by poorer adult incubation attentiveness. However, as addling was the single most important cause of egg failure in both early and late started areas, and its ultimate cause unknown, seasonal trends in egg loss in this study are difficult to interpret.

It is equally unclear to what extent the immature Ring-billed Gulls breeding in late-started study areas in 1977 contributed to the observed decrease in fledging success of their chicks as compared to early, mature plumaged counterparts. One might speculate that the immature gulls were inexperienced in food finding and prehension and thus had difficulty in adequately feeding their chicks. Data presented here and discussed later, indicate that chicks in late started areas (the majority of which had at

least one immature plumaged parent) grew poorly compared to early counterparts. Coulson and White (1958) found that kittiwake chicks in 2-chick broods, attended by parents breeding for the first time, grew less well than those with more experienced (older) parents and suggested that the trend was caused by the inability of the less experienced parents to adequately feed their chicks.

Immature plumaged Ring-billed Gulls were not observed breeding in either the late started area in 1976 or in the post-peak time period in 1977, yet reductions in mean clutch size, hatching success (late clutches, 1976) and fledging success (post-peak clutches, 1977) were observed in those clutches. This observation does not eliminate the possibility that the late, 1976 and post-peak, 1977 Ring-billed Gulls were on average younger than those breeding earlier but old enough not to exhibit immature plumage; however, it does suggest that seasonally varying, environmental or extrinsic factors, independent of the gulls themselves were responsible for the decrease in total reproductive success late in the season.

Perrins (1970) suggested that a seasonally decreasing food supply may be the primary cause of the seasonal decrease in chick survival observed in some avian species. Data presented here, and observations made by Kirkham (1977) indicate that general food availability or the availability of certain food items may have decreased during the 1977 breeding season on Gull Island. Late chicks in 2-chick broods grew more slowly from age 5 to 20 days than samples of early counterparts (cf. Figure 4B). Growth analysis was not carried out on chicks that died before 30 days of age, however, the majority of dead or dying chicks (at least in late started study areas) felt emaciated when handled and it was my impression that these chicks were dying or had died of malnutrition. Further evidence suggesting decreased food availability late in the 1977 breeding season was that no large broods (3- or 4- chick) were

fledged in late started study areas, while many were fledged in early started study areas (cf. Table 11). Proportionately more late chicks in 2-chick broods weighed less than 400 grams when last weighed after 30 days of age (cf. Table 12) when compared to early counterparts. This relationship was not due to generally younger (and thus smaller) chicks occurring disporportionately in the late sample and thus suggests that late chicks may have fledged at generally lower weights than early chicks.

The 'evidence' for decreasing food availability with season could readily be interpreted in terms of younger, less experienced Ring-billed Gulls breeding in late-started areas who were not as able to care for and feed their chicks as mature gulls (cf. page 85, this discussion). However, without estimates of food availability throughout the breeding season, this dilemma is difficult to resolve.

Contrary to what has commonly been found in previous gull studies (e.g., Patterson, 1965; Davis and Dunn, 1976; Parsons, 1975a), an increase in chick predation was not a factor causing decreased fledging success in either post-peak or late clutches in this study.

Finally, it is not known to what extent seasonal variations in other environmental factors such as weather or vegetation were the cause of the seasonal trends in total reproductive success reported here, but the possibility of cause and effect relationships are recognized.

As was previously mentioned, Gull Island Ring-billed Gulls deserted their eggs at night for varying lengths of time up to 10 May, 1977. This type of behaviour has been noted in Ring-billed Gulls at other breeding locations (Emlen et al., 1966; Vermeer, 1970; P. Fetterholf, pers. comm.; J. Chardine, pers. obs.) and in other larid species (Marshall, 1942; Drent, 1970; Nisbet, 1975, Hunter and Morris, 1976). However, almost no qualitative

or quantitative data are available. Hunter and Morris (1976) reported durations of nocturnal desertion in the Common Tern, of approximately 2 to 8 hours and also that each desertion and return to the colony occurred synchronously among most terns in the colony. Most authors agree that the observed nocturnal desertions were caused by a nocturnal predator of some type (e.g., Black-crowned Night Heron, Great Horned Owl (Bubo virginianus), Racoon (Procyon lotor)). Hunter and Morris (1976) offered direct evidence that this was the case in their ternery. On 23 April, 1977, on Gull Island I found a wing feather of a Great Horned Owl lying next to a decapitated, adult Ring-billed Gull. Furthermore, several decapitated Ring-billed Gulls were found on Gull Island during the 1978 breeding season (G. Fox, pers. comm.). These observations suggest that the Great Horned Owl is a nocturnal predator on Gull Island and further that the activities of this predator may have been a proximate factor causing the nocturnal desertion observed in 1977. Similarly, Vermeer (1970) reported finding the feathers of a Great Horned Owl in areas of his colony where decapitated Ring-billed Gull adults and chicks were found.

The possible effect of nocturnal desertion on hatching success has been previously discussed. In addition this study brings to light two possible consequences of nocturnal desertion to the reproductive biology of the Ring-billed Gull that may suggest selection pressure on early nesting gulls to desert their eggs at night. The effects of this behaviour on incubation period will be discussed first, followed by its effects on intra-clutch hatching synchrony.

One would expect the temperature of nocturnally deserted Ring-billed Gull eggs to rapidly drop below that which is necessary for embryonic development (cf. Hunter et al., 1976). In general, nocturnally deserted eggs would therefore be retarded in development compared to continuously incubated eggs

and as a result take longer to hatch (cf. Hunter et al., 1976). Furthermore, one would expect a direct relationship between the total duration of nocturnal desertion experienced by an egg and its incubation period. Since the total duration of nocturnal desertion decreased with the date of egg laying (cf. Figure 7), incubation period should likewise decrease with time of season. Data presented here showed that the incubation period of a clutch did in fact decrease with the date of clutch completion (cf. Figure 5). It is possible to predict the approximate amount of incubation period extension by simply finding the total duration of nocturnal desertion experienced by the third egg in a 3-egg clutch. For example, a clutch completed on 15 April, 1977, experienced a minimum total duration of nocturnal desertion of 150 hours or about 6.25 days. A given 3-egg clutch completed on 15 April, 1977, had an incubation period of approximately 31 days or approximately 6 days over the base incubation period for the Ring-billed Gull of about 25 days (Vermeer, 1970; this study).

MacRoberts and MacRoberts (1972) and Parsons (1972) reported similar decreases in incubation period with season, for Herring and Lesser Black-backed Gulls. Changes in climate and parental attentiveness related to the time of season, may have been responsible for the seasonal decrease in incubation period (MacRoberts and MacRoberts, 1972) while Parsons (1972) showed that a seasonal decrease in egg size may have also been a causative agent. In my study, nocturnal desertion would probably not have been as effective in extending the incubation period had the temperatures on Gull Island in April and early May been higher, thus reducing the cooling effect of incubation interruption.

The net effect of increasing incubation period with progressively earlier dates of clutch completion was to reduce the variability in the

hatching distribution of a particular area, compared to the distribution of clutch starts. In other words, inter-clutch hatching synchrony was enhanced. Although pre-peak clutches were initiated earlier than peak clutches, the proportionately longer time they took to hatch (cf. Figure 5) over clutches initiated later, resulted in pre-peak chicks hatching temporally closer to peak chicks. A further implication of the observed relationship between incubation period and date of clutch completion (or more generally, date of egg laying) in nocturnally deserted study areas, is that incubation period will decrease with the laying order of eggs within a clutch. Given that the length of the laying period does not change over the season (cf. Table 16) one may predict from the above relationship of laying order and incubation period that nocturnally deserted clutches would hatch over a shorter period of time than constantly incubated clutches. Indeed, the hatching periods of 3-egg clutches in early started areas (where nocturnal desertion predominantly occurred) were shorter, and thus the intra-clutch hatch more synchronous, than counterparts in late started areas (where nocturnal desertion generally did not occur (cf. Table 15)). Thus nocturnal desertion acted to enhance intra-clutch hatching synchrony through its effect on incubation period. Additional evidence for this contention is given in Table 17, where it was shown that in 3-egg clutches initiated late enough in the early-started areas to experience only short periods of nocturnal desertion (or none at all, cf. Appendix 1) most took two or more days to hatch and were thus classed as asynchronous. A seasonal decrease in the level of intra-clutch hatching has been reported in the Common Tern (Nisbet and Cohen, 1975; Courtney, in press). These authors also suggested that nocturnal desertion occurring early in the season, was responsible in part for this trend.

Even the most lengthy single nocturnal desertions (approximately 10

hours -occurring prior to 22 April) could only account for a net incubation period differential between successively laid eggs in a clutch of about 20 hours (since eggs are laid on average every two days). Clearly, other factors, acting in conjunction with nocturnal desertion, were involved in causing the intra-clutch hatching synchrony observed in early-started areas in 1977. Figure 6 shows a depression in diurnal incubation attentiveness during the laying period of pre-peak and peak 3-egg clutches while no such depression occurred in late counterparts. Although the sample size of hours analyzed was generally low in the laying period, the data suggest that reduced diurnal incubation attentiveness of early nesting Ring-billed Gulls, may have contributed to intra-clutch hatching synchrony, early in the season. In summary, nocturnal desertion behaviour acted to enhance both inter- and intra-clutch hatching synchrony in early-started study areas in 1977.

Nocturnal desertion behaviour has rarely been discussed in terms of its adaptive significance, although Drent (1970) suggested that the behaviour functions as a predator avoidance mechanism. I have no data with which to refute or support Drent's contention, however, the many references indicating the proximate cause of nocturnal desertion to often be a nocturnal predator do suggest an anti-predator function of this behaviour. In addition, I suggest that nocturnal desertion is of adaptive significance through its effects on inter- and intra-clutch hatching synchrony. Empirical evidence generally shows that colonial gulls initiating clutches at a time when the majority of gulls in the colony are also doing so (i.e., at the peak of clutch starts) reproduce more successfully than either earlier or later breeding gulls. By deserting their eggs nocturnally, pre-peak Gull Island Ring-billed Gulls may reduce the possibly detrimental effects of breeding before the peak (cf. Patterson, 1965) by hatching their eggs temporally closer

to the hatching of peak clutches. Indeed this study showed that pre-peak chicks grew at comparable rates and fledged equally successfully as peak chicks. The generally 'tighter' hatching synchrony over the whole colony, as a result of nocturnal desertion, may be of benefit not only to pre-peak gulls but to individuals in the colony as a whole. Darling (1938) suggested that breeding synchrony is adaptive in that it proportionately reduces chick predation rates (assuming constant predator pressure) by reducing the time span within which the chicks in the colony are at a vulnerable age. It is a moot point as to whether predator pressure remains constant in the face of prey increases, but if so, Darling's model further suggests that there is a positive relationship between the degree of breeding synchrony and its beneficial effects.

The general intra-clutch hatching synchrony observed in early started areas and probably in part caused by nocturnal desertion behaviour may also be of adaptive significance. The evolutionary significance of hatching patterns has mainly been discussed in terms of (intra-clutch) hatching asynchrony as an adaptation to facilitate brood size adjustment when food availability is low (Lack, 1954). In an asynchronous hatching clutch, the last chick to hatch (C-chick from 3-egg clutch) is at an age and hence size disadvantage with respect to its siblings and thus may be competitively inferior in terms of obtaining food (cf. Langham, 1972). Egg size may also be important in determining how small and thus, competitively inferior the last chick to hatch is, with respect to its siblings (Parsons, 1975b). I found increased mortality of C-chicks (from 3-egg clutches) as compared to brood mates, in late, predominantly asynchronous hatching clutches, whereas, no significant differences were found in either the total reproductive success of each egg in early, predominantly synchronous hatching clutches (cf. Table

14) or the growth patterns of A, B and C chicks from those clutches (cf. Figure 4A). It is of course not known whether it was the asynchronous hatching pattern, per se, that caused C-chicks to do so poorly in late clutches or a factor such as reduced food availability late in the season. Possibly, both factors were acting together (as theory predicts) to cause the observed brood reduction. However, I suggest that when food availability is high (presumably when early chicks are being raised) it may be advantageous to hatch a clutch synchronously rather than asynchronously. Thereby, the chances of brood reduction are decreased because each chick is of approximately the same age. The relatively small differences in size among such brood mates, as a consequence of intra-clutch differences in egg size would result in correspondingly small differences in competitive ability and a generally higher fledging success than if the intra-clutch hatch were asynchronous (cf. Parsons, 1975b).

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Appendix

Appendix 1: Nocturnal desertion data from study areas 1, 2, and 3 from 1977

Study Area 1

Date	Time Off (EST) $\bar{X}$	SE (hours)	Time On (EST) $\bar{X}$	SE (hours)	Clutches Deserted n	Proportion of total monitored	Mean Duration of Nocturnal Desertion (hours, mins)
15 April	19:05	0.004	04:58	0.004	4	1.00	9, 53
16	19:17	0.004	05:00	0	4	1.00	9, 43
17	19:15	0	04:58	0.029	4	1.00	9, 43
18	19:20	0.004	05:04	0.220	4	1.00	9, 44
19	19:12	0.175	04:57	0.095	4	1.00	9, 45
20	19:34	0.045	04:55	0.007	7	1.00	9, 21
21	19:41	0.045	05:13	0.178	7	1.00	9, 32
22	No nocturnal desertion						
23	22:24	1.222	04:53	0	3	1.00	6, 29
24	24:26	0.075	04:41	0.167	2	0.67	4, 15
25	20:46	0.116	04:25	0.040	7	1.00	7, 39
26	20:47	0.034	04:21	0.034	9	1.00	7, 34
27	23:21	0.052	04:23	0.004	8	1.00	5, 02
28	No data						
29	No data						
30	No data						
1 May	No data						
2	22:53	0.003	23:51	0.009	9	1.00	0, 58
3	22:22	0.003	04:02	0.042	9	1.00	5, 40
4	20:19	0.059	04:03	0.004	9	1.00	7, 44
5	21:39	0.377	23:30	0.379	4	0.44	1, 51
6	21:50	0.080	23:43	0.008	8	0.89	1, 53
7	No nocturnal desertion						
8	19:23	1.112	20:47	1.070	3	0.33	1, 51
9	21:00	0.026	02:33	0.025	9	1.00	5, 33
10	21:32	0.063	03:04	0.569	4	0.44	5, 32

Study Area 2

Date	Time Off (EST) $\bar{X}$	SE (hours)	Time On (EST) $\bar{X}$	SE (hours)	Clutches Deserted n	Proportion of total monitored	Mean Duration of Nocturnal Desertion (hours, mins)
20 April	19:37	0.007	04:54	0.004	4	1.00	9, 17
21	19:31	0	05:16	0.381	3	1.00	9, 45
22	No nocturnal desertion						
23	21:34	0.042	04:53	0	2	1.00	7, 19
24	01:27	0	04:30	0	1	0.25	3, 03
25	21:22	0.012	04:40	0.187	4	1.00	7, 18
26	21:12	0.147	04:23	0.126	4	1.00	7, 11
27	23:25	0.011	04:22	0.008	4	1.00	4, 57
28	No data						
29	No data						
30	No data						
1 May	No nocturnal desertion						
2	21:56	0.019	23:10	0.982	4	1.00	1, 14
3	22:26	0.021	04:01	0.005	4	1.00	5, 35
4	20:26	0.010	04:03	0	3	1.00	7, 37
5	21:15	0	23:03	0.403	3	1.00	1, 48
6	No nocturnal desertion						
7	No nocturnal desertion						
8	No nocturnal desertion						
9	23:35	0.209	02:30	0	2	0.67	2, 55

Study Area 3

Date	Time Off (EST) $\bar{X}$	SE (hours)	Time On (est) $\bar{X}$	SE (hours)	Clutches Deserted n	Proportion of total monitored	Mean Duration of Nocturnal Desertion (hours, mins)
20 April	19:37	0.003	04:54	0.003	6	1.00	9, 17
21	19:31	0	05:25	0.227	6	1.00	9, 54
22	No nocturnal desertion						
23	21:37	0.088	04:52	0.007	4	1.00	7, 15
24	01:48	0.550	04:30	0.017	2	0.67	2, 42
25	22:09	0.890	04:22	0	6	1.00	6, 13
26	20:54	0.079	04:17	0.042	6	1.00	7, 23
27	23:25	0.026	04:20	0.003	5	1.00	4, 55
28	21:53	0.024	04:13	0.012	12	1.00	6, 20
29	25:50	0.002	04:06	0.013	12	1.00	6, 16
30	21:55	0.003	04:07	0.017	12	1.00	6, 12
1 May	No nocturnal desertion						
2	22:03	0.058	22:14	0.010	17	0.94	0, 11
3	22:30	0.009	04:02	0.028	19	1.00	5, 32
4	20:47	0.046	04:01	0.002	18	1.00	7, 14
5	No nocturnal desertion						
6	22:16	0.029	23:55	0.234	9	0.47	1, 39
7	No nocturnal desertion						
8	No nocturnal desertion						
9	23:15	0.378	01:55	0.324	11	0.58	2, 40